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COVER: Wilson's Snipe (*Gallinago delicata*). Illustration by Scott Rashid.

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FRONTISPIECE. Evermann's Rock Ptarmigan (*Lagopus muta evermanni*), endemic to the Near Islands in the western Aleutians, were reintroduced to Agattu from Attu to reestablish a breeding population. Translocations during 2003–2006 were successful as translocated birds survived, nested, and produced young which survived until recruitment in successive breeding seasons. Photograph of a male during the breeding period by Steve E. Ebbert.

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DEMOGRAPHY OF A REINTRODUCED POPULATION OF EVERMANN'S ROCK PTARMIGAN IN THE ALEUTIAN ISLANDS

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ABSTRACT.—We report results of a 4-year translocation effort to reestablish a breeding population of Evermann's Rock Ptarmigan (*Lagopus muta evermanni*) in the Near Islands group of the western Aleutian Archipelago. Habitat restoration was completed by eradication of introduced foxes from Agattu Island by 1979. We captured and moved 75 ptarmigan from Attu Island to Agattu Island during 2003–2006, and monitored 29 radio-marked females in the last 2 years of the study. We compared the demography of newly translocated birds (n = 13) with resident birds established from translocations in previous years (n = 16). Mortality risk was increased by translocation and 15% of females died within 2 weeks of release at Agattu Island. All surviving females attempted to nest but initiated clutches 8 days later in the breeding season and laid 1.5 fewer eggs per clutch than resident females. Probability of nest survival ($\bar{x} \pm$ SE) was good for both translocated (0.72 ± 0.17) and resident females (0.50 ± 0.16), and renests were rare. Probability of brood survival was higher among translocated (0.85 ± 0.14) than resident females (0.25 ± 0.12), partly as a result of inclement weather in 2006. Fecundity, estimated as female fledglings per breeding female, was relatively low for both translocated (0.9 ± 0.3) and resident females (0.3 ± 0.2). No mortalities occurred among radio-marked female ptarmigan during the 10-week breeding season, and the probability of annual survival for females in 2005–2006 was between 0.38 and 0.75. Translocations were successful because females survived, successfully nested, and recruited offspring during the establishment stage. Post-release monitoring provided useful demographic data in this study and should be a key component of translocation programs for wildlife restoration. Future population surveys and additional translocations may be required to ensure long-term viability of the reintroduced population of ptarmigan at Agattu Island. *Received 31 July 2008. Accepted 16 July 2009.*

Reintroductions and other translocations are an important tool for restoring and enhancing plant and animal populations within their native geographic range (Griffith et al. 1989, Snyder et al. 1999, Ewen and Armstrong 2007). Greater effort may be allocated to moving animals if resources are limited, rather than to post-release monitoring needed to evaluate project success. However, post-release monitoring is critical because it allows estimation of the demographic parameters needed to evaluate status of reintroduced populations. Population models can then be used to evaluate the effects of removals on source populations, and management strategies and

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environmental factors which may affect the eventual success or failure of newly established populations (Sarrazin and Legendre 2000, Armstrong et al. 2007, Dimond and Armstrong 2007, Reynolds et al. 2008).

Translocations have been widely used with continental populations of upland gamebirds. Release of wild-caught birds has been used to establish new breeding populations of White-tailed Ptarmigan (*Lagopus leucura*) (Braun et al. 1978, Hoffman and Giesen 1983, Clarke and Johnson 1990) and Ruffed Grouse (*Bonasa umbellus*) (Moran and Palmer 1963, Kurzejeski and Root 1988). Reintroductions have been used to bolster declining or isolated populations of prairie grouse (*Tympanuchus* spp.) (Snyder et al. 1999, Coates et al. 2006) and Greater Sage-Grouse (*Centrocercus urophasianus*) (Reese and Connelly 1997, Baxter et al. 2008). Translocations have also been an essential component of applied conservation for populations of birds on oceanic islands, including waterfowl (Reynolds et al. 2008), flightless rails and parrots (Clout and Craig 1995, Jamieson and Wilson 2003), and songbirds (Komdeur 1994, Armstrong et al. 2002, Robertson et al. 2006, Ewen and Armstrong 2007). Restoration of insular populations poses particular challenges because life-history traits of island and mainland vertebrates can be highly divergent with differences in demography, behavior, and morphology (Stamps and Buechner 1985, Blondel 2000). For example, island populations of waterfowl, grouse, and songbirds tend to breed later, lay smaller clutches of larger eggs, and have higher adult survival than mainland populations (Mercer 1967, Blondel 1985, Rohwer 1988, Atwood et al. 1990, Blondel et al. 1992, Wiggins et al. 1998).

The Aleutian Archipelago of western Alaska consists of >450 isolated islands with large populations of breeding seabirds. Historically, the Aleutian Islands had no native terrestrial mammals west of Umnak Island (Murie 1959). Island populations of birds were negatively impacted by deliberate introductions of arctic fox (*Alopex lagopus*) by fur trappers between 1750 and 1940 (Maron et al. 2006). Depredation of eggs, young, and breeding birds led to steep population declines and local extirpation of waterfowl, seabirds, and terrestrial birds on islands where foxes were present (Bailey 1993). The U.S. Fish and Wildlife Service (USFWS) began systematic removal of foxes in 1949, as part of recovery efforts for Aleutian Cackling Geese (*Branta hutchinsii leucopareia*), as well as seabirds of conservation concern (Springer et al. 1977, Byrd et al. 1997, Williams et al. 2003).

Rock Ptarmigan (*Lagopus muta*) are arctic-breeding grouse with a Holarctic distribution (Holder and Montgomerie 1993); eight subspecies have been described from the Aleutian Islands based on allopatric distributions and phenotypic differences in plumage coloration (Holder et al. 2000, 2004). Evermann's Rock Ptarmigan (*L. m. evermanni*) is an endemic subspecies confined to the Near Islands group in the western Aleutian Archipelago. It is the only subspecies where males have a black nuptial plumage (Frontispiece), and has unique population genetics that distinguish it from all other subspecies of Rock Ptarmigan in the Aleutians and elsewhere (Holder et al. 2000). Evermann's Rock Ptarmigan were historically present on all islands in the Near Islands group but introduced foxes reduced their range to Attu Island and an estimated population size of ~1,000 birds (Ebbert and Byrd 2002). Arctic fox are still present on the islands of Nizki-Alaid and Shemya but were eradicated from Agattu Island and Attu Island by 1979 and 1999, respectively (Bailey 1993, Ebbert and Byrd 2002). Evermann's Rock Ptarmigan, due to their limited geographic range and small population size, have been designated birds of special management concern by the USFWS.

We report results from a field study of a newly established island population of Evermann's Rock Ptarmigan. Prior to our project, comprehensive surveys by the Alaska Maritime National Wildlife Refuge indicated that ptarmigan and foxes were absent on Agattu Island. Ptarmigan may disperse across marine waters (Zimmerman et al. 2005), but natural recolonization across the 28 km strait between the islands of Attu and Agattu had not occurred in the 25-year period since foxes were eradicated. Thus, we translocated wild-caught ptarmigan over a 4-year period and conducted intensive post-release monitoring at Agattu Island in the last 2 years of the project. Ecological studies of Rock Ptarmigan in the Aleutians have been limited to studies of molt and diet of *L. m. gabrielsoni* at Amchitka Island (Jacobsen et al. 1983, Emison and White 1988), and our project is the first demographic study of an island population of ptarmigan in Alaska. Our main goal was to compare the demographic rates of translocated and resident ptarmigan, and to evaluate the

efficacy of translocations for restoration of insular populations of landbirds. A secondary goal was to compare life history traits between insular and mainland populations of Rock Ptarmigan that might influence translocation success for subspecies endemic to the Aleutian Islands.

METHODS

Study Area.—Attu (52.85° N, 173.19° E; 89,279 ha) and Agattu (52.43° N, 173.60° E; 22,474 ha) are in the Near Islands group in the western range of the Aleutian archipelago and part of the Alaska Maritime National Wildlife Refuge. Attu is a mountainous island with steep hillsides rising from sea level to elevations >600 m (highest point: 861 m). Most of the land mass of Agattu Island is <230 m in elevation but a mountain range composed of seven major submassifs lies along the north side and extends from Armeria Bay eastward to Krugloi Point (highest point: 693 m). The dominant plant community in the Near Islands is maritime tundra because the climate is consistently cool, wet, and windy (Maron et al. 2006). Mean minimum and maximum temperatures are 6.5 and 9.2° C, total precipitation is 6.8 cm per month, and wind velocities average 42 kph in the 3-month period from June to August (climate data from Shemya Island, 30 km northeast of Agattu Island). Glaucous-winged Gulls (*Larus glaucescens*) and Common Ravens (*Corvus corax*) were potential predators of eggs and chicks, whereas Peregrine Falcons (*Falco peregrinus*) and Snowy Owls (*Nyctea scandiaca*) were a threat to adult ptarmigan (Gibson and Byrd 2007). Agattu Island does not have introduced species of rats (*Rattus* spp.), which are a problem elsewhere in the Aleutian Islands (Major et al. 2006).

Translocations.—Five translocations from Attu Island were conducted to reintroduce Evermann's Rock Ptarmigan to Agattu Island: four during May to June, 2003–2006 and one during September 2003. Translocations could not be conducted at other times of year in this remote area because logistical support was not available and environmental conditions were hazardous. Ptarmigan were live-captured at Attu Island using noose poles, noose carpets, and ground nets. Birds were held for up to 48 hrs in fiberglass transport containers and provided small pieces of melon as a source of food and water. The 28-km strait between the islands of Attu and Agattu required 3 hrs to traverse on the research vessel M/V Tiglax. Ptarmigan were immediately released upon arrival at Agattu Island at one of three sites: McDonald Cove on the east coast (2003), Karab Cove on the south coast (2004–2005), or Binnacle Bay on the north coast (2006). Loss of body mass of translocated ptarmigan was measured by subtracting mass at release from mass at capture. We adjusted the difference in body mass by egg mass (21 g per egg, Holder and Montgomerie 1993) in cases where females laid eggs during the holding period. Necropsies of birds that died during handling or after release were conducted shortly after recovery of the carcass by a wildlife veterinarian (W. P. Taylor, Alaska Fish and Game Department).

Field Methods.—We conducted post-release monitoring at Agattu Island from late May to mid-August in 2005 and 2006 to estimate the fecundity and survival of female Evermann's Rock Ptarmigan (Kaler 2007). Our study sample included newly translocated birds and resident ptarmigan encountered at Agattu Island. The resident population included marked birds surviving from previous translocations and their unmarked offspring. All ptarmigan released were individually banded and color banded with batch marks (2003–2004) or individual band combinations (2005–2006) at first capture. Yearlings and adults were distinguished by patterns of pigmentation and shape of the wing primaries (Weeden and Watson 1967). Females were fitted with radio transmitters attached with either a bib (2005: 15 g, Telemetry Solutions, Concord, CA, USA) or a necklace harness (2006: 6 g, Holohil Ltd., Carp, ON, Canada). Radio transmitters had a battery life of 12–18 months and were equipped with mortality switches to facilitate detection of dropped transmitters and mortality events. Radio-marked birds were tracked with a portable radio receiver (R2000, Advanced Telemetry Systems, Isanti, MN, USA) and 3-element Yagi antenna. We started radio-tracking immediately after release and relocated females daily by radio triangulation until nests were located. All points were recorded in Universal Transverse Mercator (UTM) coordinates using a hand-held Global Positioning System receiver (Garmin GPSmap 76; Garmin International, Olathe, KS, USA).

Nests of translocated ptarmigan were located by radiotelemetry whereas nests of resident ptarmigan were located by searching suitable nest habitat around roosts of males, which often acted as sentinels (Holder and Montgomerie 1993).

Unmarked females were captured with noose poles on territories or with dip nets at nest sites, and were marked with radio transmitters. We did not examine the eggs if a nest was discovered during egg-laying and returned after the clutch had been completed. We counted the eggs, if a nest was discovered during incubation, measured (± 0.1 mm) length (L) and width (W) of all eggs, and floated the eggs in a small cup of lukewarm water to estimate stage of incubation (Westerskov 1950). Buoyancy of eggs was related to stage of incubation as: flat on the bottom of the container = 0 days, 45° = 5 days, 90° = 10 days, floating at surface = 13 days, and a ~18 mm diameter circle protruding above the water surface = 18 days. The onset of hatching was detected by days 19, 20, and 21 of incubation by tapping, raised star-shaped pips in the egg shell, and hole-pipped eggs, respectively.

Female nest attendance was checked every 3–4 days during incubation by triangulating the radio signal at distances >30 m from the nest site. Nests were visited every 1–2 days around the predicted hatching date to capture young and ascertain nest fate. We considered nests to be *abandoned* if a female ceased nest attendance during egg-laying or incubation, *depredated* if the eggs were destroyed or removed before the expected hatch date, and *successful* if egg shells with detached membranes were left in the nest bowl after the chicks had departed or if we captured at least one chick at or near the nest. We counted offspring in broods <15 days of age with binoculars from >50 m and flushed broods 2–3 times at 15–25 days of age to calculate survival of young after hatching.

Demographic Parameters.—Demographic performance of ptarmigan is, at times, affected by female age or annual conditions (Watson 1965, Steen and Unander 1985, Gardarsson 1988, Novoa et al. 2008). Our sample sizes were small and we pooled data across age classes and years to compare the demography of translocated and resident Rock Ptarmigan. We calculated 10 demographic parameters for breeding females (after Sandercock et al. 2005).

(1) Date of clutch initiation was calculated by backdating from stage of egg-laying, stage of incubation, or the date of hatching. We assumed that Rock Ptarmigan laid one egg/day, started incubation on the penultimate egg, and had an average incubation period of 21 days (Holder and Montgomerie 1993).

(2) Total clutch laid (TCL) was the total number of eggs laid in the clutch, recorded during the first visit to the nest during incubation.

(3) Egg volume (V) was estimated from linear measurements of ptarmigan eggs using $V = kLW^2$, where $k = 0.49$ for Willow Ptarmigan (*L. lagopus*), L = egg length, and W = egg width (Sandercock and Pedersen 1994). We calculated average egg volume per clutch because eggs within a nest were not independent observations.

(4) Nest survival until hatching (NEST) was the probability that at least one egg hatched and produced a chick that departed the nest. Values of NEST < 1 included total clutch losses due to abandonment and predation.

(5) Renesting (RENEST) was the probability that a female laid a replacement clutch, conditional upon loss of her first clutch.

(6) Chicks/egg laid (C/E) was the percentage of eggs laid that eventually hatched and produced chicks that left the nest. C/E was calculated only for nests that survived incubation and hatched at least one egg. Values of C/E < 1 included partial clutch losses due to eggs that disappeared during incubation and eggs that survived incubation but failed to hatch.

(7) Brood survival until fledging (FLED) was the probability that at least one chick survived from hatching until fledging at 15–25 days of age. Fledglings completed growth of juvenal feathers by 2 weeks and began to evade observers with short flights instead of running and hiding. Values of FLED < 1 were due to total brood failure, which was readily ascertained by the behavior and movements of females. If females lost their brood, they flushed during approach by an observer or joined small groups of failed breeders.

(8) Fledglings/chick hatched (F/C) was the percentage of hatched chicks that left the nest and survived until fledging at 15–25 days. F/C was calculated only for broods that survived the brood-rearing period and fledged at least one chick.

(9) Seasonal survival of females was calculated by monitoring radio-marked females over the 10-week breeding season. We left-censored a 2-week acclimation period to control for potential effects of higher mortality rates immediately following stress of capture,

transport, release in a new environment, and attachment of the radio transmitter.

(10) Annual survival of females was calculated from the return rates of radio-marked birds from 2005 to 2006. We conducted intensive searches of territories for all radio-marked females in 2006. Birds relocated alive in 2006 were known survivors whereas radio transmitters recovered near scattered feathers or carcass remains were considered known mortalities. Female fate was unknown if birds were not relocated or if radio transmitters were recovered without accompanying remains.

Estimation of Fecundity.—We calculated a synthetic estimate of fecundity (F) as the expected number of female fledglings produced per breeding female per year. We controlled for possible nest losses before discovery by an observer, and differences in renesting rates, by first calculating the number of eggs surviving until hatching for each breeding female (E):

$$E = (\mathrm{TCL}_1 \times \mathrm{NEST}) + ([1 - \mathrm{NEST}] \times \mathrm{RENEST} \times \mathrm{TCL}_2 \times \mathrm{NEST})$$

where TCL_n = total clutch laid, subscripts 1 and 2 are values for first nests and renests, NEST = probability of nest survival, and RENEST = probability of renesting after clutch loss. We calculated fecundity (F) as:

$$F = E \times \mathrm{C/E} \times \mathrm{FLED} \times \mathrm{F/C} \times 0.5$$

where E = the number of surviving eggs, C/E = percentage of chicks hatched/egg laid, FLED = probability of brood survival until fledging, F/C = percentage of fledglings produced/chick leaving the nest, and 0.5 is the proportion of females based on a 1:1 sex ratio.

Statistical Analysis.—Comparisons of demographic parameters between translocated and resident females were conducted using statistical procedures in Program SAS (Version 8.1, SAS Institute Inc., Cary, NC, USA). Sample sizes differed among some components of fecundity because we lacked complete information for a few nests and losses to predators caused attrition over the breeding season. Continuous data were compared with two sample t-tests and frequency data were compared with contingency tests. *Post hoc* comparisons of survival rates were conducted with Program CONTRAST (USGS, Patuxent Wildlife Research Center, Laurel, MD, USA). All tests were two-tailed and considered significant at $\alpha < 0.05$. Means ± SE are presented.

We estimated daily survival rates of nests and broods during the incubation and brood-rearing periods with the nest survival procedure of Program MARK (Version 4.1, G. C. White, Colorado State University, Fort Collins, CO, USA). We collected data for nests for a 63-day exposure period from 1 June until 2 August, and for broods for a 38-day exposure period from 28 June until 5 August. We created encounter histories for each nest and brood survival analyses with five types of information (Dinsmore et al. 2002): (1) the day the nest or brood was found (k), (2) the last day it was known to be active (l), (3) the last day it was checked (m), (4) the fate (f) where 0 = successful and 1 = depredated, and (5) the number of nests or broods with the same encounter history (n). All assumptions of the nest survival model were met in this study (Kaler 2007).

We considered five candidate models in our analyses of nest and brood survival. We expected that translocated females might have lower nest survival rates than resident females, and daily survival rates might vary during the breeding season. Survival rates of ground nests of precocial birds might be expected to vary seasonally if vegetative cover changes, poorly concealed nests are selectively destroyed, or predator activity is affected by nest densities and availability of alternative prey (Klett and Johnson 1982, Dinsmore et al. 2002, Wilson et al. 2007). Similarly, brood survival rates might be lowest after nest departure and improve as chicks begin to thermoregulate and fly. Thus, our global model included the effects of female group (translocated vs. resident), a linear effect of time, and the interaction of these factors ($S_{\mathrm{group} \times \mathrm{linear}}$). We also fit reduced models with main effects ($S_{\mathrm{group + linear}}$), single factors ($S_{\mathrm{group}}$, S_{time}), and a model that constrained daily survival to be a constant (S_{constant}). Global models are saturated in the nest survival model, and adjustments for overdispersion are not possible because the variance inflation factor (c) is not identifiable (Dinsmore et al. 2002). All models were fit to the data using design matrices and the logit-link function in Program MARK.

Model selection was based on an information theoretic approach (Burnham and Anderson 1998). The model with the lowest Akaike's

Information Criterion corrected for small sample sizes (AIC_c) value was the best fit and models with $\Delta AIC_c \leq 2$ were equally parsimonious. We based inference on differences in deviance in cases where the difference in number of parameters was one ($\Delta K = 1$). We used ratios of Akaike weights to quantify the extent of support among models (w_i/w_j).

We calculated parameter estimates with unconditional variances with the model-averaging procedure of Program MARK to examine seasonal variation in daily survival rates. We extrapolated daily survival rates using $\hat{S}^{dur}$, where $\hat{S}$ = the daily survival rate of nests or broods, and *dur* = the duration of the nesting or brood-rearing stages to obtain stage-specific estimates of the probabilities of nest and brood survival. For example, the duration of an eight-egg nesting attempt was 28 days, calculated as the duration of the egg-laying (8 days) and incubation periods (21 days) with incubation starting after laying of the penultimate egg (−1 day). The duration of the brood-rearing period was 20 days. Variances of stage-specific estimates were calculated using the delta method, following formulae and methods described by Powell (2007).

We used parametric bootstrapping to obtain confidence intervals for our synthetic estimates of fecundity (*F*) (Gotelli and Ellison 2004). We generated bootstrap distributions using tools of Program MATLAB (Version 6.5, MathWorks, Natick, MA, USA). Estimates of means and variances were taken directly from our parameter estimates with the exception of the probability of renesting where the variance was estimated as $\text{Var}(p) = p(1 - p)/n$, where p is the probability and n is the total sample size. Total clutch laid was modeled as draws from a normal distribution whereas probabilities were modeled as draws from beta distributions to bound draws within the range of 0 and 1. We drew a set of seven demographic rates at random for each bootstrap replicate, combined the estimates to calculate fecundity, and repeated these steps for 1,000 bootstrap iterations. Bootstrapping of fecundity was conducted separately for translocated, resident, and pooled females. We generated a distribution of differences between random pairs of bootstrap values for translocated and resident females to compare groups, and calculated a *P*-value by recording the number of bootstrap differences that were greater than the observed difference between means (Gotelli and Ellison 2004).

TABLE 1. Number of Evermann's Rock Ptarmigan translocated from Attu Island to Agattu Island, Aleutian Archipelago, Alaska, in May to June 2003–2006 and September 2003.

Year	Males	Females	Juveniles	Totals
2003	11	13	2	26
2004	11	16	0	27
2005	4	10	0	14
2006	5	3	0	8
Totals	31	42	2	75

RESULTS

We translocated 75 Evermann's Rock Ptarmigan from Attu Island to Agattu Island over a 4-year period (2003–2006, Table 1). We monitored reproduction and survival rates of 29 radio-marked female ptarmigan (translocated: $n = 13$; resident: $n = 16$) from late May to mid-August during a 2-year radiotelemetry study (2005–2006). The proportion of females that were adults was higher among translocated (92%, $n = 13$) than resident birds (56%, $n = 16$, Fisher's Exact test, $P = 0.044$), but age-classes were pooled for analyses because sample sizes were small. Our study sample included 28 nests (translocated: $n = 10$; resident: $n = 18$, including 2 renests) and 21 broods (translocated: $n = 8$; resident: $n = 13$).

Translocations.—Female ptarmigan translocated from Attu to Agattu Island in 2005–2006 ($n = 13$) were in breeding condition: 30.8% had partial brood patches and 46.2% laid an egg in the holding containers during transport. Female mass at capture averaged 568 ± 16 g ($n = 31$) and translocated females lost an average of 9% of their total body mass ($\bar{x} \pm$ SE loss: −57 ± 15 g, $n = 12$). Only one mortality occurred during the holding and transport periods in the 4-year period. A juvenile male died during holding but we were unable to assign cause of death at necropsy. Two mortalities occurred at Agattu Island during post-release monitoring in the last 2 years of the study. In both cases, radio-marked females died within 2 weeks of release. One female was recovered 2 days after release 390 m from the release site and necropsy indicated that she drowned in a small tundra pool. A second female was recovered 10 days after release 914 m from the release site; evidence at the recovery site indicated she was killed by a raptor. Release site had little effect on translocation success because surviving birds quickly dispersed to settle in alpine habitats at the northern part of Agattu Island.

TABLE 2. Demographic parameters of translocated and resident Evermann's Rock Ptarmigan at Agattu Island, Aleutian Archipelago, Alaska, 2005–2006. The first three parameters were calculated for first nests only. Data are presented as means ± SE (*n*).

Parameter	Translocated	Resident	Pooled	Statistic	$P \leq$
Date of clutch initiation (days)	16 June ± 1.0 (10)	8 June ± 1.3 (16)	11 June ± 1.2 (26)	$t_{24} = -4.5$	0.001
Total clutch laid (eggs)	6.8 ± 0.3 (10)	8.3 ± 0.2 (15)	7.7 ± 0.2 (25)	$t_{25} = 4.2$	0.001
Mean egg volume (cm^3)	23.1 ± 0.6 (8)	23.3 ± 0.2 (16)	23.2 ± 0.2 (24)	$t_{22} = 0.41$	0.68
Probability of nest survival	0.724 ± 0.166 (10)	0.500 ± 0.155 (18)	0.588 ± 0.118 (28)	$\chi^2_1 = 1.8$	0.18
Probability of renesting	0 (2)	0.50 (4)	0.33 (6)	Fisher's Exact	0.47
Chicks/egg laid (%)	85.7 ± 4.6 (8)	82.3 ± 5.1 (13)	83.6 ± 3.5 (21)	$t_{19} = -0.5$	0.66
Probability of brood survival	0.849 ± 0.139 (8)	0.251 ± 0.123 (13)	0.470 ± 0.119 (21)	$\chi^2_1 = 10.4$	0.002
Fledglings/chick hatched (%)	48.5 ± 1.1 (7)	53.9 ± 3.8 (4)	50.4 ± 0.7 (11)	$t_9 = 0.4$	0.73
Fecundity (female fledglings/ breeding female/year)	0.9 ± 0.3	0.3 ± 0.2	0.5 ± 0.2	Bootstrap	0.48

Timing of Clutch Initiation, Total Clutch Laid, and Egg Volume.—All translocated females that survived the 2-week acclimation period initiated clutches on Agattu Island. The interval between release and onset of egg-laying was 13.1 ± 0.9 days for translocated females ($n = 10$). The average date of clutch initiation was 16 June for translocated females, which was 8 days later than an average date of 8 June for resident hens (Table 2). Total clutch laid in first nests by translocated females (6.8 eggs) was 1.5 eggs smaller than the average clutch size of resident hens (8.3 eggs). Mean egg volume did not differ between resident and translocated females, and averaged 23.2 cm^3 overall.

Nest Survival, Renesting, and Chicks/Egg.—We used encounter histories from 28 nests (10 translocated and 18 resident, 2 females included in both years) to estimate daily survival rates for nests. Nests were monitored over a 63-day exposure period (day 1 = 1 June). The minimum AIC_c model contained a linear effect of time over the breeding season (S_{linear}, Table 3). The minimum AIC_c model had 1.3–2.4 times greater support than the other candidate models but all five models were equally parsimonious ($\Delta AIC_c < 1.8$).

The slope coefficient for the linear effect indicated that nest survival declined over the breeding season (from model S_{linear}: $\hat{\beta} = -0.07 \pm 0.04$, logit scale), particularly in the latter part of

TABLE 3. Model selection results for daily survival rates (*S*) of nests and broods of Evermann's Rock Ptarmigan at Agattu Island, Aleutian Archipelago, Alaska, 2005–2006. Model fit was described by the number of parameters (*K*), model deviance (Dev), Akaike's Information Criterion corrected for small sample size (AIC_c), deviations from the minimum-AIC_c model (ΔAIC_c), and Akaike weights (w_i). Models for daily survival (*S*) included comparisons of resident vs. translocated birds (group), a seasonal effect of time (linear), factorial (×) and main effects models (+), and a reduced model with no effects (constant). Exposure periods were 63 days for nesting (day 1 = 1 June) and 38 days for brood-rearing (day 1 = 28 June).

Model	*K*	Dev	AIC_c	ΔAIC_c	w_i
Nests					
S_{linear}	2	51.5	55.5	0.00	0.300
$S_{constant}$	1	54.0	56.0	0.54	0.229
$S_{group + linear}$	3	50.2	56.3	0.76	0.205
$S_{group \times linear}$	4	48.9	57.0	1.52	0.140
S_{group}	2	53.2	57.2	1.74	0.126
Broods					
S_{group}	2	43.2	47.2	0.00	0.443
$S_{group \times linear}$	4	39.7	47.9	0.68	0.316
$S_{group + linear}$	3	43.1	49.3	2.02	0.162
$S_{constant}$	1	49.7	51.8	4.52	0.046
S_{linear}	2	48.4	52.4	5.20	0.033

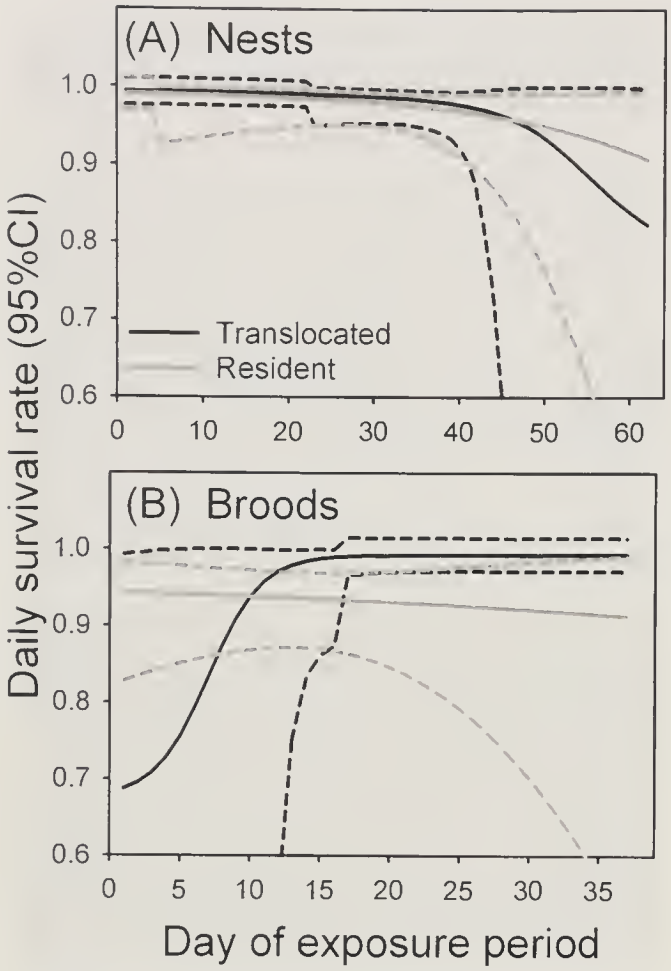

FIG. 1. Daily survival rates for nests and broods of translocated and resident female Rock Ptarmigan at Agattu Island, Alaska, 2005–2006 (n = 27 nests and 21 broods). Estimates were calculated by model-averaging in Program MARK. Exposure periods were 63 days for nesting (day 1 = 1 June) and 38 days for brood-rearing (day 1 = 28 June).

the season (Fig. 1A). Estimates of daily survival rates (from model S_{group}) revealed that nest survival was similar for translocated ($\hat{S}$ = 0.988 ± 0.008) and resident females ($\hat{S}$ = 0.976 ± 0.011), and was high overall (from model $S_{constant}$: $\hat{S}$ = 0.981 ± 0.007). Extrapolation of daily survival rates over the duration of a nesting attempt (27 to 28 days for 7- to 8-egg clutches) yielded estimates of the probability of nest survival that were 0.724 ± 0.166 for translocated females, 0.500 ± 0.155 for resident females, and 0.588 ± 0.118 for all females combined.

Six first nesting attempts failed because of nest predation or abandonment. Two resident females that renested lost their first nests 2 days before onset of incubation and at 12 days of incubation, and initiated renests after intervals of 13 and 11 days, respectively. Clutch size of the two renests was 5 and 6 eggs. Translocated and resident females that did not renest lost their nests at more advanced stages of incubation (12–23 days, n = 4). The percentage of viable eggs that hatched and produced 1-day old chicks did not differ between resident and translocated females, if the nest survived incubation, and was 83.6% overall.

Brood Survival and Fledglings per Chick.—We used encounter histories from 21 radio-marked females that successfully hatched young (8 translocated and 13 resident, 1 female included in both years) to estimate daily survival rates for broods. Broods were monitored over a 34-day exposure period (day 1 = 28 June). The minimum AIC_c model included an effect of group with a difference between translocated and resident birds (S_{group}, Table 3). Two additional models with interactive and additive effects between group and a linear effect of time ($S_{group \times linear}$, $S_{group + linear}$) were equally parsimonious or nearly so ($\Delta AIC_c <$ 2.02), but the minimum AIC_c model had 1.4–2.7 times greater support.

The slope coefficient for the effect of group (from model $S_{group \times linear}$: $\hat{\beta}$ = 6.87 ± 6.71, logit scale) was larger than the linear effect of time ($\hat{\beta}$ = 0.53 ± 0.51) or the interaction of the two factors ($\hat{\beta}$ = −0.57 ± 0.51). Brood survival of translocated females was initially low and increased over the exposure period, whereas resident birds had moderate brood survival (Fig. 1B). Overall estimates of daily survival rates (from model S_{group}) indicated brood survival was higher among translocated females ($\hat{S}$ = 0.992 ± 0.008) than resident hens ($\hat{S}$ = 0.933 ± 0.022). Daily survival rates of broods for all females combined (from model $S_{constant}$: $\hat{S}$ = 0.963 ± 0.012) were not different from the daily survival rates of nests ($\hat{S}$ = 0.981 ± 0.007, χ^2_1 = 1.71, P = 0.19). Extrapolation of daily survival rates over the duration of brood-rearing (20 days) yielded estimates of the probability of brood survival that were 0.849 ± 0.139 for translocated females, 0.251 ± 0.123 for resident females, and 0.470 ± 0.119 for all females. The percentage of chicks that successfully fledged if the brood survived the brood-rearing stage did not differ between resident and translocated females, and was 50.4% overall.

Fecundity.—We combined our estimates of demographic parameters to calculate a synthetic estimate of fecundity that controlled for nest exposure before nest discovery and productivity from renests. Fecundity tended to be higher among translocated birds (F = 0.9 ± 0.3 female fledglings/female) than residents (F = 0.3 ± 0.2), but the difference was not significant (Table 2).

Survival of Females.—We monitored seasonal survival during the nesting and brood-rearing period for 26 female ptarmigan (10 translocated and 16 resident). All females survived the 10-week breeding season and no mortalities were observed during either 2005 or 2006. We searched during the 2006 breeding season for 16 females that had been radiomarked in 2005 to assess overwinter female survival. Of the 16 females, 37.5% were detected alive, 31.3% were dead recoveries, and 31.3% were not relocated. The frequency of known mortalities was equivalent in translocated (30%, $n = 10$) and resident females (33%, $n = 6$, Fisher's Exact test, $P = 1.0$). Surviving females had strong site fidelity and distance between nest locations in consecutive years averaged 123 ± 34 m ($n = 5$). We intensively searched female territories and our minimum estimate of annual survival would be 0.38 if all missing females had died. However, if missing females survived to disperse elsewhere on the island, annual survival of females could be as high as 0.75.

DISCUSSION

Our field study is one of the first investigations of the effects of translocation on an insular population of an upland gamebird, and we provide the first estimates of demographic parameters for any of the subspecies of Rock Ptarmigan that are endemic to the Aleutian Archipelago. Our major conclusions were: (1) translocations had negative impacts on female performance with short-term increases in female mortality, delays in the timing of clutch initiation, and reductions in clutch size; (2) settlement was rapid and unaffected by location of the release sites; (3) translocated and resident females had similar rates of fecundity and survival during the period of population establishment; and (4) island and mainland populations appear to have similar demography, which may have contributed to the success of our reintroductions.

Effects of Translocation on Fecundity.—The negative impacts of translocation from Attu Island to Agattu Island were transitory and had little net effect on productivity. Logistics constrained us to hold birds for up to 48 hrs, but mortality rates were low during holding (1.4%) and comparable to translocations of other grouse (0%, Hoffman and Giesen 1983; 2.1%, Baxter et al. 2008) and waterfowl (0%, Reynolds et al. 2008). Rock Ptarmigan lost an average of 9% of body mass during transport, and similar rates of loss have been reported for translocated Ruffed Grouse (10%, Kurzejeski and Root 1988) and Laysan Ducks (*Anas laysanensis*) (6%, Reynolds et al. 2008). The only mortalities among radio-marked Rock Ptarmigan were two females that died shortly after release. Mortality rates of wildlife are often higher immediately after translocation, because of the physiological stress of captivity or elevated predation risk due to lack of familiarity with a new environment or attachment of a radio transmitter (Musil et al. 1993, Clout and Craig 1995, Armstrong et al. 1999, Baxter et al. 2008).

Ptarmigan settled quickly into alpine habitats during the establishment stage and all surviving females initiated clutches shortly after release. Future translocations of ptarmigan in the Aleutian Islands can select release sites based on safety of coastal landings without concerns about proximity to suitable habitats. In other species, translocated birds often range widely after release in search of suitable habitat or conspecifics (Musil et al. 1993, Armstrong et al. 1999, Coates et al. 2006), and long distance movements can contribute to higher mortality rates during the acclimation period (Kurzejeski and Root 1988). Our releases may have had greater success because post-release movements were constrained by the limited area of alpine habitat on Agattu Island and habitat quality was restored to historical conditions by eradication of introduced predators. Translocations of birds in breeding condition during the nesting season facilitated rapid settlement and early reproduction, similar to previous releases of ptarmigan (Braun et al. 1978). Translocations of juveniles during the nonbreeding season might have less impact on a source population but could delay establishment because juveniles must survive to the next breeding season and, at times, have lower success as first time breeders (Kurzejeski and Root 1988, Sarrazin and Legendre 2000, Robertson et al. 2006, Baxter et al. 2008, Reynolds et al. 2008).

Translocated females delayed clutch initiation and laid clutches that were 1.5 eggs smaller than nests of resident Evermann's Rock Ptarmigan. Reduced clutch size could have been due to interruptions in egg-laying if translocated females were determinate egg-layers that failed to replace missing eggs laid in clutches at Attu Island or in the handling crates during transit (Sandercock 1993). Alternatively, smaller clutches could have been due to the physiological stress of translocation. White-tailed Ptarmigan breeding in years of

harsh environmental conditions delay egg-laying and take more incubation breaks to maintain body condition (Wiebe and Martin 2000). Only resident females renested after nest failure in our study. However, females that failed to renest lost their clutches at more advanced stages of incubation when the probability of renesting was presumably low (Robb et al. 1992). Evermann's Rock Ptarmigan laid fewer eggs in renests than first nests, similar to other populations of ptarmigan (Brodsky 1986, Cotter 1999, Sandercock et al. 2005).

Translocated and resident ptarmigan differed primarily in demographic parameters that were recorded at the start of the nesting cycle. The potential demographic impacts of differences in timing of laying and clutch size were largely offset by reproductive losses. Nest and brood survival are expected to improve over the season if vegetative cover increases or predators locate offspring in vulnerable sites earlier in the season (Klett and Johnson 1982, Wilson et al. 2007). Survival of ptarmigan broods at Agattu Island increased during the breeding season, but survival of nests was lowest during the latter part of the exposure period. The lowest rates of daily survival for ptarmigan nests and broods coincided with the hatching period of Aleutian Cackling Geese and increased foraging activity by Glaucous-winged Gulls at inland sites. Gulls primarily hunted for goose eggs and goslings, but incidental predation could have reduced the fecundity of ptarmigan. Predation could potentially be a limiting factor for ptarmigan populations because gull populations are maintained at high levels in the Aleutian Islands by access to refuse from fish processing facilities (Gibson and Byrd 2007).

Ptarmigan young have limited ability to thermoregulate or evade predators in the week after hatching (Scherini et al. 2003, Hannon and Martin 2006). Increases in late season survival of broods could have been due to development of homeothermy and mobility among ptarmigan young or to more favorable climatic conditions during the latter part of the exposure period (Aulie 1976, Steen and Unander 1985). Hatching and fledging success were high, if ptarmigan young survived incubation or brood-rearing, and there was no evidence of deleterious effects caused by inbreeding depression (Briskie and Macintosh 2004).

Synthesis of the major components of reproductive effort showed that fecundity of Evermann's Rock Ptarmigan was relatively low at <1 fledgling per breeding female, and that translocated females did not have lower fecundity than resident females in our reintroduced population. If any difference occurred, it was that translocated birds tended to have higher productivity, similar to previous reports for Takahe (*Porphyrio hochstetteri*) (Jamieson and Wilson 2003). Some variation in productivity could have been explained by female age class and annual variation in demographic rates. Our sample of translocated birds included a high proportion of adults, which at times, have higher reproductive success than yearling Rock Ptarmigan (Steen and Unander 1985, but see Cotter 1999, Scherini et al. 2003). Similarly, annual fecundity of Rock Ptarmigan can be variable and influenced by local environmental factors, including food, predation, and climate (Watson 1965, Gardarsson 1988, Novoa et al. 2008). If conditions are favorable for several consecutive years, ptarmigan numbers should exhibit the exponential growth often reported for populations established by island translocations (Moran and Palmer 1963, Klein 1968, Komdeur 1994, Armstrong et al. 2002).

Survival Rates.—Seasonal survival of female Evermann's Rock Ptarmigan during the breeding period was 100% as no mortalities were observed. Mortality rates during the breeding season are higher in populations of Rock Ptarmigan where mammalian predators and Gyrfalcons (*Falco rusticolus*) are a threat (23%, Gardarsson 1988; 14%, Cotter et al. 1992; 12%, Scherini et al. 2003). Annual survival of female Evermann's Rock Ptarmigan was between 0.38 and 0.75 for one interval (2005–2006), and all losses occurred during the fall or winter after we had departed from Agattu Island. Raptors capable of killing adult ptarmigan occurred at relatively low densities during the breeding season (Kaler 2007). Seasonal mortality rates of mainland populations of Willow Ptarmigan are usually highest in autumn during raptor migration (Smith and Willebrand 1999, Hannon et al. 2003). Seasonal mortality rates of Evermann's Rock Ptarmigan may have been higher outside of the breeding season if Snowy Owls and Peregrine Falcons relied on coastal seabirds during summer but spent more time foraging at inland sites during fall and winter (Gibson and Byrd 2007). Our conservative estimate of annual survival of 0.38 for Evermann's Rock Ptarmigan is comparable to estimates of 0.37 to 0.43 for arctic and alpine populations of Willow Ptarmigan (Sandercock et al. 2005).

TABLE 4. Estimates of five demographic parameters for island (I) and mainland (M) populations of Rock Ptarmigan.

Location	Pop.	Lat.	Date of clutch initiation	Clutch size	Probability of nest survival	Probability of brood survival	Probability of adult survival	Source
Alaska, USA	I	53° N	8 June	8.3	0.59	0.47	0.38–0.75	This study
Iceland	I	66° N		>10.4	>0.90		0.26–0.82	Gardarsson 1988
Norway	I	78° N		7.5	0.44			Steen and Unander 1985
Italy	M	46° N	10 June	6.8	0.50	0.18–0.67		Scherini et al. 2003
Scotland, UK	M	57° N	Mid June	6.6	0.90	0.62		Watson 1965
Alaska, USA	M	65° N		7.0	0.67	0.81	0.26–0.71	Weeden 1965
NWT, Canada	M	68° N	11 June	8.8				Brodsky 1986, 1988
NWT, Canada	M	69° N	9 June	8.7	0.64	0.53	0.43–0.82	Cotter 1991, 1999

Life-history Traits of Ptarmigan.—Evermann's Rock Ptarmigan are endemic to oceanic islands and are a unique insular form with a black nuptial plumage and distinct population genetics (Holder et al. 2000, 2004). We found little evidence that selection on demography has contributed to development of an insular syndrome in the life-history traits of this subspecies, despite distinct differences in morphology. Compared to mainland and island populations of Rock Ptarmigan elsewhere in their Holarctic range, Evermann's Rock Ptarmigan had similar dates of clutch initiation in mid-June, intermediate values for clutch size, and comparable estimates of the probabilities of survival for nests, broods, and adults (Table 4). Evolution of an insular syndrome among the life-traits of vertebrates is frequently attributed to differences in predation and climate regimes between island and mainland sites (Mercer 1967, Stamps and Buechner 1985, Blondel 2000). Isolation reduces the diversity of predator communities and climatic conditions can be less variable due to proximity to coastal waters. These two ecological factors may have had less influence on Evermann's Rock Ptarmigan because the Near Island group supports several species of avian predators and has extreme climatic conditions associated with an exposed location in the northern Pacific Ocean (Maron et al. 2006, Gibson and Byrd 2007). Most of the geographic variation in life-history traits of Rock Ptarmigan and congeneric species appears to be driven by latitudinal and altitudinal gradients in ecological conditions in arctic and alpine environments (Sandercock et al. 2005, Novoa et al. 2008).

CONSERVATION IMPLICATIONS

Ten features of our project have been identified as factors predicting translocation success for terrestrial vertebrates (Griffith et al. 1989, Snyder et al. 1999, Ewen and Armstrong 2007). Evermann's Rock Ptarmigan are a herbivorous, native gamebird with high reproductive potential that breed as yearlings. We translocated multiple batches of wild-caught birds over a 4-year period, and birds were released into high quality habitat in the core of their historical range which had been restored by eradication of introduced predators. High survival during the breeding season, successful nesting, and recruitment of young birds indicated successful reestablishment of an island population. Small initial populations can risk extinction because of demographic stochasticity, loss of genetic diversity, and inbreeding depression. However, annual surveys in June using playbacks of male vocalizations recorded 26–27 territorial male Evermann's Rock Ptarmigan each year at Agattu Island in 2008–2009, following completion of our field study. An adaptive management strategy based on regular surveys and supplementary translocations will ensure the long-term population viability of Evermann's Rock Ptarmigan at Agattu Island.

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APPARENT SURVIVAL OF BREEDING WESTERN SANDPIPERS ON THE YUKON-KUSKOKWIM RIVER DELTA, ALASKA

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ABSTRACT.—We used 8 years of live recapture data (1998–2005) to estimate apparent annual survival for male (n = 237) and female (n = 296) Western Sandpipers (*Calidris mauri*) breeding on a 36-ha plot on the Yukon-Kuskokwim River Delta, western Alaska. Apparent annual survival (Φ) is the product of true survival and site fidelity, and estimates of Φ were corrected for the probability of encounter. Overall return rates (individual returned to the study site in a subsequent season) were lower for females (40%) than males (65%), as was Φ ($\pm$ SE, females = 0.65 $\pm$ 0.05, males = 0.78 $\pm$ 0.03), and encounter rate (females = 0.51 $\pm$ 0.07, males = 0.74 $\pm$ 0.04). Results differed from previous estimates of Φ for this species as our estimates of Φ were higher for both males and females compared to estimates from another breeding site and two nonbreeding locations. Disparity among Φ estimates from breeding and nonbreeding areas highlights the need to delineate site-specific factors throughout the annual cycle that influence population dynamics of the Western Sandpiper. *Received 30 May 2009. Accepted 9 October 2009.*

Twenty-one percent of the world's 155 shorebird species are listed as species of conservation concern by Birdlife International (Piersma et al. 1997, Johnson and Oring 2002, Sandercock 2003). Several long-term studies have revealed population declines among migratory shorebirds (Charadriiformes) in Europe (Tucker and Heath 1994, Hagemeijer and Blair 1997), North America (Howe et al. 1989, Morrison et al. 2001, Haig et al. 2005), and Asia (Rose and Scott 1997). The Western Sandpiper (*Calidris mauri*) is considered a species of high conservation concern despite being one of the most abundant shorebirds in the Western Hemisphere (Bishop et al. 2000, Morrison et al. 2000, Brown et al. 2001). Declining numbers during spring (Butler and Lemon 2001) and fall migration surveys (Neil 1992, Butler and Lemon 2001) at staging areas in British Columbia and Texas coupled with a limited breeding distribution and threats to nonbreeding habitat have led to this conservation assessment (Brown et al. 2001, Fernández et al. 2006). However, reported declines in numbers at staging sites may be caused by shifts in migration patterns and not impacts of demographic rates on population growth (Ydenberg et al. 2004).

The life history of migratory shorebirds is generally characterized by delayed maturity, low productivity, and relatively high adult survivorship (Evans and Pienkowski 1984, Piersma and Baker 2000). Robust estimation of demographic parameters is central to understanding population dynamics of avian species (Eberhardt 1985, Lande 1988, Clobert and Lebreton 1991). Estimation of survival rate is particularly important because the persistence of any animal population is the result of a balance between recruitment of new breeders into the population via reproduction and immigration, and losses due to the emigration and mortality of established breeders (Lebreton et al. 1993, Lieske et al. 2000). Estimation of these parameters and identification of ecological factors that affect avian populations requires long-term studies of marked individuals (Lebreton and North 1993).

A better understanding of shorebird demography would facilitate conservation efforts; however, population models have been developed for only a few shorebird species. Sensitivity analyses have found that adult survival often has the highest elasticity value and potentially the greatest impact on population growth rates (Hill and Carter 1991, Hitchcock and Gratto-Trevor 1997, Reed et al. 1998, Plissner and Haig 2000, Larson et al. 2002, Sandercock 2003). Effective conservation of migratory shorebirds requires reliable estimates of annual survival rates, but estimates are available for <10% of shorebird species worldwide (Sandercock 2003).

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Western Sandpipers breed along the coasts of western Alaska and eastern Siberia and are distributed over a large geographic area in nonbreeding areas ranging on the Pacific Coast from California to Peru, and on the Atlantic Coast from New Jersey to Suriname (Wilson 1994). Male Western Sandpipers spend the nonbreeding season at more northerly latitudes compared to females (Page et al. 1972, Harrington and Haase 1994, Buenrostro et al. 1999, Nebel et al. 2002), and males generally precede females north during spring migration (Holmes 1971, Senner et al. 1981, Butler et al. 1987) with the opposite pattern during fall migration (Butler et al. 1987, Ydenberg et al. 2005). Comparative studies within their nonbreeding distribution have revealed divergent life history strategies (O'Hara et al. 2005). Juveniles and females from the southern portion of the nonbreeding range are more likely to remain at nonbreeding sites during their first breeding season compared to adults and males at northerly sites. This suggests Western Sandpiper life history varies with first-year females favoring increased survival and first-year males emphasizing initial breeding opportunities (O'Hara et al. 2005). Given the species' expansive geographic distribution and age-and gender-speeific variation in life history strategies, it is likely Western Sandpipers likewise exhibit region-, age-, and gender-specific variation in survival.

Our objective was to produce estimates of apparent annual survival at a representative breeding site in the middle of the breeding range of Western Sandpipers in western Alaska. We used 8 years of live recapture data to examine whether apparent annual survival rate varied between males and females at our study site, and whether apparent survival varied significantly during the course of this study. We compare our estimates with those from a more northerly breeding site and two nonbreeding sites.

METHODS

Study Area and Field Methods.—We studied breeding Western Sandpipers at the Yukon Delta National Wildlife Refuge's Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (61° 22′ N, 165° 07′ W). We used a 36-ha study plot in dry upland tundra habitat along the Kuyungsik River (lowland moist low scrub community, Jorgenson and Ely 2001) to address our objectives. The study site supports an average of 80 breeding pairs annually (Johnson et al. 2005). Two to four observers searched this study plot daily from early May through late July from 1998 to 2005 for banded birds, nests, and broods. We banded each adult at the nest with a U.S. Geological Survey identification band and unique color combinations (3 UV-stable color bands/bird). We recaptured all birds when band loss or discoloration occurred (2% of all banded birds), indentified the individual by its U.S. Geological Survey identification band, and re-banded the bird with new color bands. Adults were classified as male or female by culmen length during banding (>93% of all birds; Page and Fearis 1971, Carter 1984). Birds were classified as males or females via behavior (courtship displays, copulation position) and comparison with their mate (females > males) when culmen length was inconclusive (24–25 mm). Locations of nests and banded individuals were mapped using geographic information system layers in ArcGIS (ESRI 2007) and nests were monitored through hatch, predation, or abandonment. It is possible to differentiate first-year Western Sandpipers that hatched in the previous breeding season from birds that are ≥2 years old based on plumage charaeteristics (Sandercock et al. 1999). However, our sample of first-year birds was limited (24% of females and 17% of males banded were first-year birds), and previous attempts to estimate apparent survival in this population revealed unacceptable overdispersion when fitting age-specific models to the data set ($\hat{c} > 8$; M. Johnson, unpubl. data). We chose not to estimate apparent survival by age class (i.e., first-year and ≥2 year old birds), and instead estimated apparent survival for all breeding adults.

Statistical Analyses.—We used Cormack-Jolly-Seber mark-recapture models to estimate apparent annual survival (Φ) corrected for probability of encounter (p). Apparent survival rate was the probability that a bird alive in breeding season i survived until the following breeding season ($i + 1$) and returned to our study plot. Encounter probability was the probability that we detected a bird given that it was alive. Losses from the breeding population may result from permanent emigration or mortality, and are the complement of apparent survival. We conducted mark-recapture analysis following methodologies outlined by Burnham and Anderson (1998) using Program MARK (Version 4.2, Cooch and White 2004).

We incorporated gender (*sex*) and time-dependence (t) as variables in our global model of Φ and p because both parameters are known to vary

between males and females and across years in many shorebird species (Sandercock 2003). We also modeled temporal variation as a linear (*T*) and quadratic (*TT*) trend across years. Several nonexclusive factors may lead to lower apparent survival rates during the first interval after initial capture in many bird populations (Sandercock and Jaramillo 2002). Thus, we modeled Φ for the interval following initial capture (Φ^1) and all subsequent intervals (Φ^{2+}) separately for each gender (time-since-marking, or 2 age-class model). We did not expect p to vary between first and subsequent time intervals and modeled p as a function of *sex* and t. Thus, our starting global model was ${\Phi^1}_{sex*t}$, ${\Phi^{2+}}_{sex*t}$, p_{sex*t}.

We used two methods to assess the fit of our global model to the sandpiper survival data; a parametric bootstrap goodness-of-fit test, and the median $\hat{c}$ procedure in Program MARK (Cooch and White 2004). The parametric bootstrap goodness-of-fit procedure generated a bootstrap distribution of expected deviances through simulation (n = 1,000 replicates) and calculated a variance inflation factor ($\hat{c}$) as the observed deviance divided by the mean expected deviance from the bootstrap distribution (Burnham and Anderson 1998). We simulated sandpiper survival data in the median $\hat{c}$ procedure with a range of deviances (n = 1,000 replicates), and performed a logistic regression to estimate the median $\hat{c}$ value of the simulated data (Cooch and White 2004). Moderate amounts of overdispersion are common in mark-recapture analyses with $\hat{c}$ values of 1–3 indicating an acceptable global model fit (Lebreton et al. 1992).

We fit reduced models with fewer parameters to the sandpiper data set after examining the fit of our starting global model. We began the model selection process by modeling encounter probabilities followed by apparent survival probabilities. We contrasted models with one and two age classes (Φ vs. Φ^1, Φ^{2+}) after modeling p. We modeled probabilities (Φ and p) by initially dropping parameters from a factorial model to create additive models, and finally examined single factor and constant models. We assessed model fit with quasi-Akaike's Information Criterion, adjusted for small sample sizes ($QAIC_c$, Burnham and Anderson 1998). Models where $\Delta QAIC_c$ was <2 from the best fit model ($\Delta QAIC_c$ = 0) were considered equally parsimonious, and Akaike weights (w_i) were used to evaluate the relative likelihood of a model within the set of candidate models. The ratio of $QAIC_c$ weights between two candidate models was used to quantify the fit of a particular model to the data relative to other models (Burnham and Anderson 1998). We applied the variance components procedure in Program MARK to obtain overall estimates of apparent survival and encounter probability. We used the model averaging procedure in Program MARK to obtain annual estimates of apparent survival. Finally, we calculated the distance between annual nest attempts for site-faithful males, females, and reuniting pairs, and used analysis of variance by ranks to contrast inter-annual dispersal distances for these three groups (Kruskal and Wallis 1952). We report means ± SE.

RESULTS

We individually marked 533 breeding Western Sandpipers (296 females, 237 males) in the first 7 of 8 years of study. Overall return rates (individual returned to the study site in a subsequent season) were lower for females (40%) than males (65%). Both goodness-of-fit methods detected minor overdispersion when we fit our global model to the sandpiper survival data set (parametric bootstrap goodness-of-fit procedure $\hat{c}$ = 2.9; median $\hat{c}$ procedure $\hat{c}$ = 1.4). These two estimates differ, but both indicated that our global model was a satisfactory starting point ($\hat{c} \leq 3.0$), and we chose the more conservative estimate of overdispersion ($\hat{c}$ = 2.9) and continued with model selection. We systematically varied $\hat{c}$ between the two estimates after completing model selection and found no differences among the top performing models, regardless of which $\hat{c}$ value was used.

Model selection based on $QAIC_c$ indicated the best-fit model was where survival and encounter probabilities differed between males and females but were constant over time (Φ_{sex}, p_{sex}, Table 1). Apparent survival rate of females (0.65 ± 0.05) was lower than for males (0.78 ± 0.03) as was encounter rate (females = 0.51 ± 0.07, males = 0.74 ± 0.04). Model selection revealed moderate support for a negative linear time trend model that varied between males and females ($\Phi_{sex + T}$, p_{sex}; $\Delta QAIC_c$ = 1.3; $\Phi_{males\ 1998–2004}$ = 0.82 − 0.75, $\Phi_{females\ 1998–2004}$ = 0.69 − 0.60), but all 95% confidence intervals surrounding point estimates of annual apparent survival were overlapping. There also was support for a time-since-marking (2 age-class) model with variation between males and females (${\Phi^1}_{sex}$ ${\Phi^{2+}}_{sex}$, p_{sex}; $\Delta QAIC_c$ = 1.6; Φ^1,

TABLE 1. Mark-recapture models for annual estimates of apparent survival for adult Western Sandpipers breeding near Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska, 1998–2005.

Model structure[b]	Model statistics[a]			
	K	Deviance	$\Delta QAIC_c$	w_i
Φ_{sex}, p_{sex}	4	122.6	0.0	0.32
$\Phi_{sex + T}$, p_{sex}	5	121.9	1.3	0.16
Φ^1_{sex} Φ^{2+}_{sex}, p_{sex}	6	120.2	1.6	0.14
$\Phi_{sex + TT}$, p_{sex}	6	120.8	2.2	0.11
Φ^1_{sex} Φ^{2+}_{c}, p_{sex}	5	123.1	2.5	0.09
Φ_{c}, p_{sex}	3	127.6	3.0	0.07
Φ_{T}, p_{sex}	4	127.2	4.6	0.03
Φ_{TT}, p_{sex}	5	126.5	5.9	0.02
Φ_{sex}, p_{c}	3	130.8	6.2	0.01
$\Phi^1_{sex + t}$ $\Phi^{2+}_{sex + t}$, p_{sex}	15	110.9	10.7	0.002
Φ_{sex*t}, p_{sex*t}	26	105.3	28.1	< 0.001
Φ^1_{sex*t} Φ^{2+}_{sex*t}, p_{sex*t}	37	97.2	43.5	< 0.001

[a] We described model fit by the number of parameters (K), deviance, and the difference in quasi-Akaike's Information Criterion ($\Delta QAIC_c$) from the best-fit model. $QAIC_c$ values were calculated using a variance inflation factor of 2.9. We present models with moderate support (Akaike weight $w_i \geq 0.01$) in order of relative fit to the best-fit model (i.e., $\Delta QAIC_c = 0$), followed by a two age-class (time-since-marking) model with additive effects of sex and time, a standard Cormack-Jolly-Seber model that did not control for time since marking, and the starting global model.

[b] Model factors included: Φ^1 = apparent survival during the first-year post banding, Φ^{2+} = apparent survival during subsequent years, Φ = annual apparent survival in models lacking age structure, c = constant, *sex* = gender, t = time or annual variation, T = linear time trend, TT = quadratic time trend, * = a factorial model, and + = an additive model.

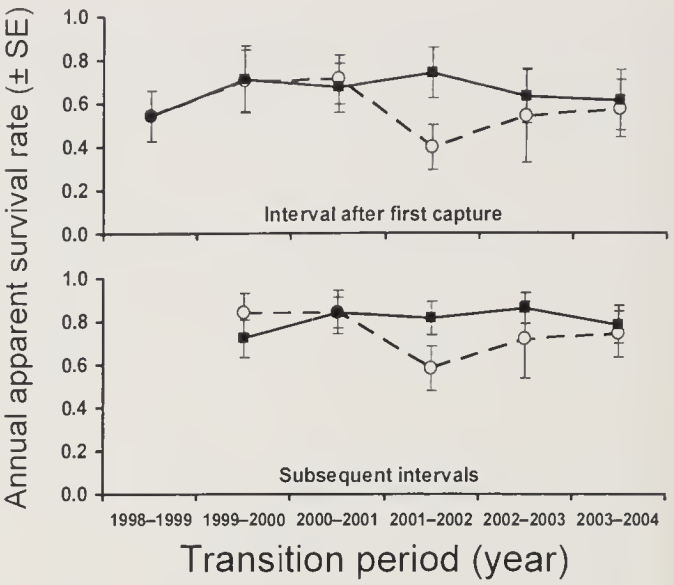

FIG. 1. Annual apparent survival rates (mean ± SE) of adult Western Sandpipers (296 females, 237 males) breeding near Kanaryarmiut Field Station, Yukon-Kuskokwim River Delta, Alaska (1998–2005) in the interval after first capture and subsequent intervals (males = squares connected with solid lines, females = circles connected with broken lines). Annual estimates were calculated via model averaging, and estimates for interval 2004–2005 were not identifiable because of the time dependence in apparent annual survival and the probability of encounter.

males = 0.72 ± 0.06, females = 0.57 ± 0.08; Φ^{2+}, males = 0.81 ± 0.04, females = 0.69 ± 0.06). However, the best-fit model (Φ_{sex}, p_{sex}) had ≥2 times the support of both of these models. Model selection did not support annual variation (t) in apparent survival rates ($\Delta QAIC_c$ = 7.3); however, we examined the point estimates of annual apparent survival from our global model (Φ^1_{sex*t}, Φ^{2+}_{sex*t}, p_{sex*t}) because time dependence is often not supported in sparse data sets. Female apparent survival was lower in 2001 compared to other years in the interval after first capture (Φ^1) and later intervals (Φ^{2+}; Fig. 1).

Inter-annual dispersal distances varied among site-faithful females, males, and reuniting pairs (χ^2_2 = 54.2, $P < 0.001$). Inter-annual dispersal distances were smallest among reuniting pairs (56.0 ± 12.3 m, n = 47 pairs). Inter-annual dispersal distances were greater among females (220.9 ± 27.7 m, n = 66) compared to males (86.9 ± 8.5 m, n = 174) for site-faithful individuals that did not reunite with their prior mate. We surveyed 29 plots (8.3-ha/plot) annually within a 29 km^2 area surrounding our study site (15–31 May, 2004–2005). We did not detect any color-marked birds during 50 hrs of observation in the surrounding region. No banded birds that went undetected in our surveys were encountered by concurrent research projects being conducted in the surrounding area (2003–2005).

DISCUSSION

We used Cormack-Jolly-Seber mark-recapture models to estimate apparent annual survival of breeding Western Sandpipers on the Yukon-Kuskokwim River Delta, Alaska. These estimates complement those from other parts of the breeding and nonbreeding range by identifying potential temporal and spatial patterns in survival rates. Apparent survival of female Western Sandpipers was lower than males, and hierarchical model selection results indicated that apparent survival did not vary annually. Previous estimates of apparent survival for breeding Western Sandpipers also were higher for males than females (Sandercock et al. 2000), but our estimates were higher for both males and females (Table 2). Two studies also have used mark-recapture techniques to estimate the apparent annual survival of Western Sandpipers in nonbreeding areas. Juvenile and adult males in Baja California had relatively low apparent annual survival (Fernán-

TABLE 2. Annual estimates of apparent survival for Western (*Calidris mauri*) and Semipalmated (*C. semipalmatus*) sandpipers from studies that used mark-recapture statistics for live encounter data.

Species	Range[a]	Age[b]	Gender[c]	Apparent survival[d]	# birds	# years[e]	Reference
Western Sandpiper	B	A	F/M	0.57	236	4	Sandercock et al. 2000
	NB	J	M	0.49	139	4	Fernández et al. 2003
		A	M	0.45	117		
	NB	J/A	F	0.62	1,990	3	Fernández et al. 2004
			M	0.54	1,383		
	B	A	F	0.65	296	8	This study
			M	0.78	237		
Semipalmated Sandpiper	B	A	F	0.56	249	8	Sandercock and Gratto-Trevor 1997
			M	0.61	237		
	B	A	F	0.59	122	4	Sandercock et al. 2000
			M	0.73	108		
	NB	A	F/M	0.65	215	4	Rice et al. 2007
		J	F/M	0.55	319	4	

[a] Range: B = breeding area, NB = nonbreeding area.
[b] Age: J = juveniles ≤1 year of age, A = adults >1 year of age.
[c] Gender: F = females, M = males.
[d] Apparent survival: estimate from best-fit model, or average of annual estimates (i.e., Sandercock and Gratto-Trevor 1997).
[e] # years = duration of study in years.

dez et al. 2003, Table 2), and females had higher rates of apparent annual survival than males in Chitré, Panama (Fernández et al. 2004, Table 2).

Our results are comparable to those from breeding areas for a sympatric *Calidris* species with similar life history characteristics. Semipalmated Sandpipers (*C. pusilla*) are small-bodied shorebirds that breed in the arctic and sub-arctic that also undertake long distance migrations and distribute themselves over a relatively large nonbreeding range (Gratto-Trevor 1992). Male Semipalmated Sandpipers near Nome, Alaska had higher apparent survival rates than females (Table 2) and both rates were similar to our estimates for Western Sandpipers. Male Semipalmated Sandpipers breeding at La Pérouse Bay, Manitoba, Canada had higher apparent survival rates than females (Table 2). These estimates were lower than ours for Western Sandpipers; however, there was considerable annual variation in that study (1980–1987, males 0.53–0.74, females 0.43–0.71; Sandercock and Gratto-Trevor 1997).

Differences between estimates of apparent survival for Western Sandpipers in this study and those from Nome may reflect temporal and/or spatial variation in survival rates. Sandercock et al. (2000) conducted their study from 1993 to 1996 at a site near Nome, Alaska. It is difficult to assess whether differences are due solely to temporal variation because the two studies were not contemporary. Survival rates vary over time in other species (e.g., Lesser Snow Goose [*Anser caerulescens*], Francis et al. 1992; Mallard [*Anas platyrhynchos*], Franklin et al. 2002; Barn Owl [*Tyto alba*], Altwegg et al. 2003), and this phenomenon may occur with Western Sandpipers. However, model selection results did not indicate apparent annual survival varied during the course of our study (Table 1).

Other researchers have demonstrated that demographic parameters including survival rates often vary spatially (e.g., Nichols et al. 1990, Kanyamibwa et al. 1993, Franklin et al. 2002, Pearce et al. 2005), and higher estimates of apparent survival at our study site may reflect site-specific conditions that promote higher survival compared to Nome, which is ~365 km and 4° latitude further north than our study site. Western Sandpipers breeding at Nome experience a shorter breeding season with longer periods of inclement weather compared to birds at our study site (Johnson and Walters 2008). A more severe climate coupled with longer annual migration distances may predispose birds at Nome to decreased survival.

Annual variation in apparent survival did not occur in our study population, even though it has been reported in other studies of Western Sandpipers that were of considerably shorter duration (4 years, Sandercock et al. 2000; 3 years, Fernández et al. 2003). Examination of point estimates from our global model revealed that female apparent survival was lower in 2001 compared to other years (Fig. 1). We are not able

to account for this variation, but lower female survival in 2001 may partially explain why overall estimates of apparent survival were lower for females compared to males.

Whether lower apparent annual survival among female Western Sandpipers represents variation in true survival or sexual variation in breeding site fidelity is unknown because we are not able to differentiate the relative influence of mortality versus permanent emigration in our estimation of apparent annual survival. Males generally exhibit greater breeding site fidelity than females among monogamous sandpipers (Oring and Lank 1982, Piersma et al. 1996). We cannot conclude that female annual survivorship is lower than for males in our study population because females may exhibit lower breeding site fidelity than males. However, average inter-annual dispersal distances were relatively small in relation to size of our study site, and similar to those reported near Nome (median inter-annual dispersal distance near Nome: reuniting pairs = 38 m, males = 48 m, females = 157 m). Further, no banded birds that went undetected in our surveys were encountered in the surrounding area. We conclude that local permanent emigration was not common at our study site.

Greater inter-annual dispersal distances among site-faithful females may indicate that females also emigrate from our study site at a higher rate than males. However, local movement patterns may or may not be indicative of larger scale dispersal patterns. Encounter probabilities were lower for females during our study, which may indicate temporary emigration (i.e., attempting reproduction at another location for 1 or more intervening years) is more common among females, or there are behavioral differences that result in lower detection rates for females. Males are more conspicuous early in the breeding season because they engage in conspicuous epigamic displays daily, whereas females are more cryptic spending greater amounts of time in concealed locations, such as wet meadows (Lanctot et al. 2000). Further, female encounter rates may be lower if only a portion of those individuals that permanently emigrate still pass through our study site before settling at other locales, or if some individuals pass through quickly and escape detection.

Western Sandpipers are a species of high conservation concern yet the underlying causes warranting this classification are unclear. Disparity between and among apparent survival estimates from breeding and nonbreeding areas highlights the need to delineate site-specific factors throughout the annual cycle that influence population dynamics of Western Sandpipers. The closely related Semipalmated Sandpiper is likely to have comparable population demographics to the Western Sandpiper (Fernández et al. 2003). Our estimates of apparent annual survival for Western Sandpipers are similar to true annual survival rates required to sustain a breeding population of Semipalmated Sandpipers (~0.80, Hitchcock and Gratto-Trevor 1997). However, observed population declines may be misleading. Reported declines in numbers at staging sites may be caused by a shift in migration patterns (Ydenberg et al. 2004) and not by a decreasing population, further underscoring the necessity of additional research to elucidate these questions. Effective modeling and predicting population trends requires accurate estimation of vital rates encompassing the range of natural variability. Our estimates of adult survival of Western Sandpipers augment and complement previous estimates by providing current estimates from a centrally located site within the species' breeding range, and serve to better inform future conservation efforts.

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NATAL PHILOPATRY AND APPARENT SURVIVAL OF JUVENILE SEMIPALMATED PLOVERS

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ABSTRACT.—Natal philopatry is rare in long-distance migrant shorebirds and requires long-term population studies to detect. We report on the rate of natal philopatry from a 18-year study of Semipalmated Plovers (*Charadrius semipalmatus*) marked as hatchlings to an arctic breeding site near Churchill, Manitoba. About 2% (27/1271) of banded hatchlings returned to the Churchill area to breed. There was no male/female bias in rates of philopatry: 17 male and 10 female hatchlings recruited into the local breeding population. The annual rate of recruitment of hatchlings varied between 0 and 10.7%. Age of first encounter on breeding areas ranged from 1 to 8 years (median age 4) suggesting either unusually delayed age at first breeding, or low detection rates for philopatric hatchlings. The maximum age of a recruited (known-age) hatchling was 9 years. Natal dispersal distances did not differ between males and females, and averaged 5 km between hatching and breeding locations. We used a time-since-marking mark-recapture model to calculate apparent survival of hatchlings. Apparent survival in the interval after first capture was $\phi_1 = 0.0475$ (95% CI: 0.030–0.075), whereas apparent survival (ϕ_{2+}) of birds during subsequent intervals was 0.866 (95% CI: 0.764–0.927). Low rates of natal philopatry suggest little advantage to site familiarity for juveniles, and agree with theoretical predictions for migratory species with widespread habitat availability. *Received 15 June 2009. Accepted 7 October 2009.*

Natal philopatry is rare in long-distance migrant birds and requires either long-term population studies or large sample sizes to detect (Thompson and Hale 1989, Renner and McCaffery 2008). Using known-age birds in survival analyses avoids the complications of assuming age of first breeding in population viability analyses and, with sufficiently large sample sizes, allows precise estimates of age-specific survival (Sidhu et al. 2007), probability of breeding (Sedinger et al. 2001, 2008), and life-expectancy (Lavers et al. 2007). Analyzing natal philopatry can also help evaluate hypotheses about the adaptive significance of gender bias in natal dispersal rates and distances (Greenwood and Harvey 1982, Weatherhead and Forbes 1994, Sutherland et al. 2000).

Studies of arctic-breeding birds are disadvantaged in documenting natal philopatry and dispersal because of inaccessibility of breeding areas and low encounter probabilities (Renner and McCaffery 2008). Possibly as a consequence, studies of temperate breeding shorebirds typically report higher rates of encounter of breeding juveniles, especially if the species is of conservation concern (e.g., *Charadrius alexandrinus* and *C. melodus*; Larson et al. 2000, Colwell et al. 2007b, Stenzel et al. 2007).

The Semipalmated Plover (*C. semipalmatus*) has been the subject of an 18-year population study near Churchill, Manitoba. This small shorebird breeds in open gravel, tundra, beaches, and riverbeds throughout the sub-arctic regions of North America (Nol and Blanken 1999). Semipalmated Plovers migrate long distances from sub-arctic breeding areas to a large, dispersed wintering range that spans coastal areas of the southern United States, Mexico, Central America, and northern and central South America. Unlike many *Charadrius* plovers, there is currently no evidence to suggest this species is declining (Morrison et al. 2006, Bart et al. 2007). An earlier study of this species suggested low rates of natal philopatry and no gender bias in these rates (Flynn et al. 1999). Our objectives are to: (1) update knowledge of these factors, (2) evaluate natal dispersal distances, and (3) estimate apparent juvenile and adult survival based on a known-age sample. We also estimate the earliest age of first breeding and report on a longevity record based on a known-age hatchling.

METHODS

Study Sites and Species.—Field work was conducted each year from the beginning of June to mid-August in 18 years including 1988 and 1992 to 2008. We regularly searched 11 major breeding sites in the area south and east of Churchill, Manitoba, Canada (58° 45′ N, 95° 04′ W), spanning ~ 20 km of coastal beaches and two inland sites in an area of 34.2 km^2 (Fig. 1). Each field season, researchers walked

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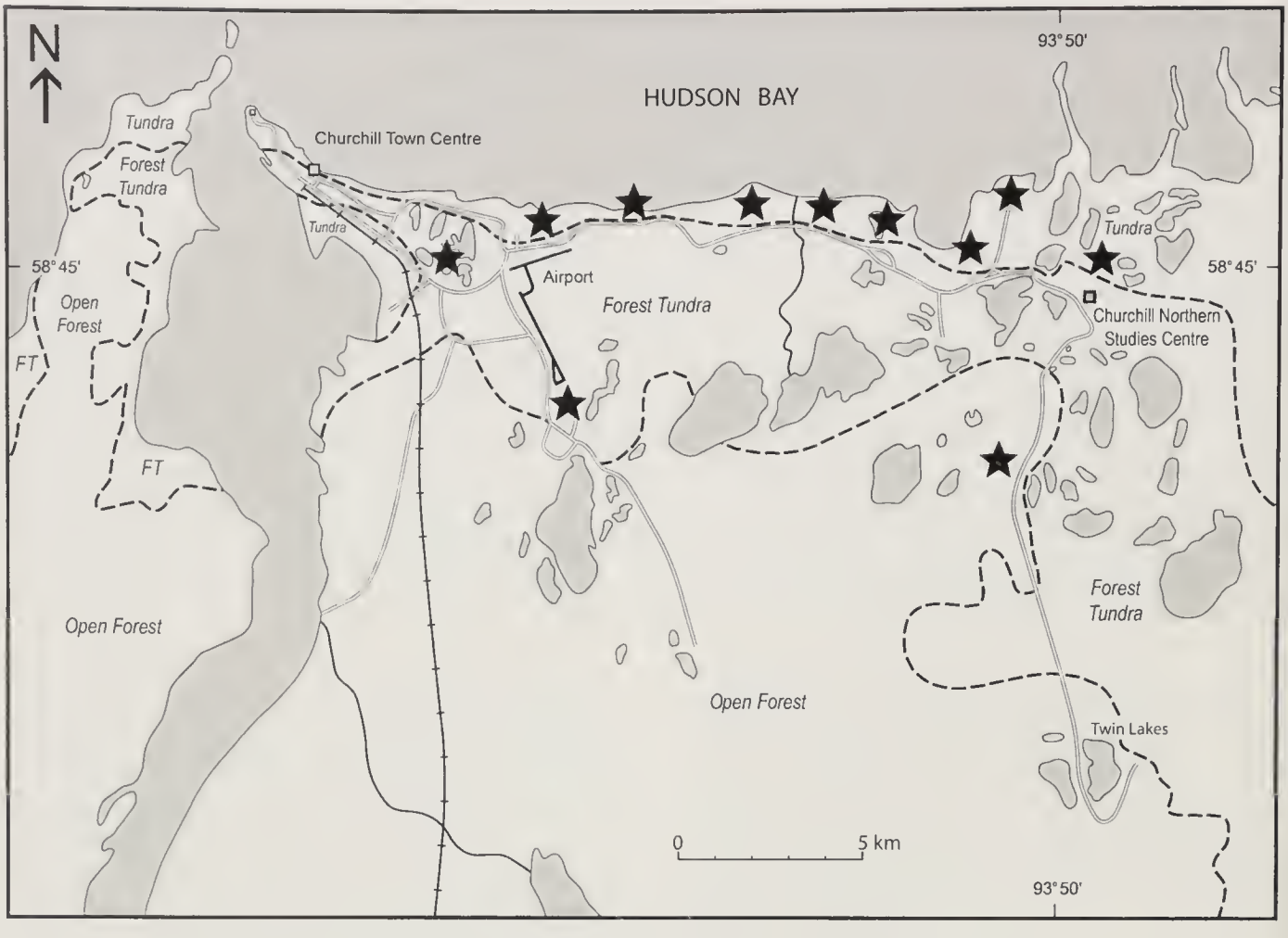

FIG. 1. Churchill, Manitoba area showing the 11 major study sites (★).

potential nesting areas in search of Semipalmated Plovers. The nests of Semipalmated Plovers in 1988 and from 1992 to 2000 were assigned identification (ID) numbers sequentially as they were found within the 11 areas, and locations of nests were drawn on field maps and aerial photos. Nests of Semipalmated Plovers were assigned ID numbers from 2001 to 2008 and the locations were recorded using a Global Positioning System (GPS). In early June, observers searched for previously banded Semipalmated Plovers and recorded the band combinations of color-marked birds using 20–40 X spotting scopes. Any nesting Semipalmated Plovers that were unbanded, or needed clarification of identification (e.g., faded color bands) were captured using circular walk-in traps with a keyhole entrance, made of hardware cloth, that were placed over the nest. Once adults were captured, they were banded with an aluminum band and given a unique color combination of bands or faded color and aluminum bands were replaced. Gender of adults was assigned using the number of brown feathers in the crown and supercilium with females having more brown feathers than males (Teather and Nol 1997). Gender assignments were confirmed by behavioral postures with males using display flights or mounting females during copulations.

Chicks were banded in the nest with unique aluminum bands and, depending on the year of study, with either brood-specific or individual color band combinations.

Statistical Analysis.—We assigned the location of the natal site as the UTM of the center of one of the 11 nesting areas for older nest and banding records without reliable GPS locations (in years prior to 2000) (Fig. 1), and the location of the first breeding site as the UTM of the center of the site at which we first encountered them breeding. We used a binomial test to examine whether there was a bias in the gender of returning hatchlings, and *t*-tests to compare natal dispersal distances of males and females.

We used a two-stage 'time-since-marking' model for live encounter data using Program MARK to calculate annual probabilities of apparent survival (ϕ) and encounter (p).. The time-since-marking model separates apparent survival in the first interval after capture (ϕ_1) from apparent survival in subsequent intervals

(ϕ_{2+}) (Larson et al. 2000). We modeled apparent survival as a function of year of marking and gender because these factors are important in other plovers (Larson et al. 2000), and treated the encounter rate as a nuisance parameter. We tested for possible overdispersion before testing reduced models by using the median $\hat{c}$ procedure to calculate a variance inflation factor for the global starting model (Cooch and White 2004).

RESULTS

Twenty-seven of 1,271 (2.1%) banded hatchlings from 1988 to 2008 returned to breed in the Churchill area. Rates of return were low in all years, but reached 10% in 2000 and 2001 (Table 1). Ten local females and 17 males recruited into the breeding population, a ratio that was not significantly different than 1:1 (Binomial test, $P = 0.09$). The age (±SE) at which birds were first encountered breeding ranged widely from 1 to 8 years (median 4 years) and did not differ between males and females (males: 3.9 ± 0.4 years, females: 4.2 ± 0.6 years; $t = 0.38$, $P = 0.65$). The maximum age of a recruited (known-age) hatchling was 9 years. The distance (±SE) between natal sites and nesting sites where we first encountered philopatric individuals did not differ between males and females (males: 5.8 ± 1.4 km, median = 4.2 km, range: 0.7 to 12.6 km, $n = 11$; females: 3.7 ± 1.8 km, median = 0.8 km, range: 0.3 to 12.7 km, $n = 7$; $t = 0.93$, $P = 0.37$).

Our estimate of $\hat{c}$ for the global model indicated there was little evidence of overdispersion ($\hat{c} < 1$), and we set the variance inflation factor to $\hat{c} = 1$ and used AIC*c* for model selection. The minimum AIC*c* model for the survival analysis from Program MARK included two capture periods for apparent survival (ϕ) and a constant encounter rate (p). Apparent survival in the first interval after capture (ϕ_1) was 0.048 (95% CI: 0.030–0.075), whereas survival (ϕ_{2+}) for birds during subsequent capture periods was 0.866 (95% CI: 0.764–0.927). Encounter probabilities (p) were relatively low, 0.174 (95% CI: 0.113–0.230). The next best model included a time effect for encounter probabilities but was 28.8 AIC*c* units from the top model and received no weight relative to the top model ($w_i < 0.01$).

TABLE 1. Number of newly banded Semipalmated Plover chicks per year and number of new adult recruits from that year's cohort.

Year	Newly banded chicks	Min. number of recruits from cohort (%)
1988	57	1 (1.75)
1992	31	0 (0)
1993	87	3 (3.44)
1994	92	1 (1.08)
1995	81	1 (1.23)
1996	106	2 (1.89)
1997	75	2 (2.67)
1998	58	2 (3.45)
1999	25	0 (0)
2000	28	3 (10.70)
2001	38	4 (10.50)
2002	44	1 (2.27)
2003	94	1 (1.06)
2004	50	2 (4.00)
2005	105	2 (1.90)
2006	103	0 (0)
2007	122	0 (0)
2008	75	0 (0)

DISCUSSION

The frequency of returning Semipalmated Plovers marked as hatchlings is among the lowest reported for shorebirds (Thompson and Hale 1989, Flynn et al. 1999). Our estimate was similar to an earlier estimate from the same study area using observation data for returning juveniles from 1988 to 1996 (1.57%, $n = 455$, Flynn et al. 1999) despite a sample size that has nearly tripled. Our hatchlings were banded within 48 hrs of hatching, and low rates may be due to high mortality in the period after hatching when young are unable to thermoregulate or fly, and are vulnerable to inclement weather conditions and predators (Thompson and Hale 1989, Flynn et al. 1999, Sandercock et al. 2005, Colwell et al. 2007a). Our survival estimates obtained for the first sample period were also low compared to that reported for the temperate congeners: Piping Plover (*C. melodus*) and Snowy/Kentish Plover (*C. a. alexandrinus*) (survival from hatching to the following year, $\phi = 0.15$, Sandercock et al. 2005; $\phi = 0.18$ for true survival of *C. a. nivosus*, Stenzel et al. 2007; $\phi = 0.32$ for *C. melodus* banded as juveniles ≥16 days of age, Larson et al. 2000). Predator control can reduce mortality of hatchlings for both temperate North American species (Stenzel et al. 2007). However, large differences between these rates and those of Semipalmated Plovers may also be due to greater permanent emigration (through greater natal dispersal) from the Churchill study area, rather than lower survival, because this population of Semipalmated Plovers appeared to be stable over the study

period (E. Nol, unpubl. data) and otherwise could probably not sustain mortality of this magnitude. The difference between these survival rates among congeners also mirrors that seen in comparing natal philopatry and dispersal rates between migratory and resident passerines (Weatherhead and Forbes 1994, Sutherland et al. 2000). Lower rates of natal philopatry in long-distance migrants like Semipalmated Plovers may be due to dispersal costs accrued when they migrate south and relinquish familiarity with their natal area. It may only be important to find similar, but not necessarily familiar habitat when they return to breed (Weatherhead and Forbes 1994).

There was substantial variability in number of recruits into the breeding season among hatchling cohorts, but a model of survival with time-dependence was not supported. A similar absence of time effects was also found for Kentish Plover in southern Turkey (Sandercock et al. 2005) and, in both cases, may have been due to sparse data with low numbers of philopatric young. Alternatively, variation in the number of recruiting individuals may be more common when resources for breeding birds fluctuate widely (e.g., Black-throated Blue Warbler, *Dendroica caerulescens*; Rodenhouse et al. 2003) or where interference competition results in exclusion of potential recruits (Arcese et al. 1992). Low fecundity of arctic-breeding shorebirds may keep populations below the carrying capacity of breeding areas (Piersma and Baker 2000), but as yet we know little about the possible role of density-dependence in this group of birds.

Territorial shorebirds are often assumed to have male-biased natal philopatry (reviewed in Colwell et al. 2007b) because of a resource-defense mating system (Greenwood 1980). However, bias towards philopatric recruiting juvenile males, where it occurs, is usually small (Gratto et al. 1985, Reed and Oring 1993, Colwell et al. 2007b, Stenzel et al. 2007; but see Redmond and Jenni 1982). The advantages of familiarity with the natal site should be approximately equal for males and females of monogamous, bi-parental incubating species. Female Snowy Plovers share in incubation duties but typically desert the brood and, at times, re-nest with other males (Page et al. 1995). In this species, where females are presumed to have a relatively low attachment to the territory, the return rate of juvenile females to the local study area to breed is only 12% lower than for juvenile males, but still 64% (Stenzel et al. 2007). This difference reversed in winter with juvenile males more likely to disperse (54%) from wintering areas than juvenile females (44%). Thus, a re-evaluation of the theoretical basis for gender-biased natal dispersal in birds is probably needed (Redmond and Jenni 1982, Sutherland et al. 2000).

Most Semipalmated Plovers appear to delay breeding beyond 1 year although, contrary to the results from the previous study on this species (Flynn et al. 1999), at least one male bred in its first year. Delayed age at maturity differs from other studies of migratory shorebirds, where most individuals attempt to breed in their first year (reviewed in Sandercock et al. 2005). This suggests that a large proportion of the Churchill population may over-summer on wintering areas (e.g., McNeil et al. 1994), similar to reports for three species of calidridine sandpipers in Africa and Central America (Summers et al. 1995, O'Hara et al. 2002).

The precise age of first breeding is difficult to ascertain because numbers of philopatric young were low and re-encounter probabilities of banded hatchlings are low (Sandercock et al. 2005). Age-specific variation in breeding propensity with higher rates of philopatry can be estimated with robust design models (Sedinger et al. 2001, 2008), but our data were not adequate for this approach. Most hatchlings were banded with an aluminum band and a single color band. Band loss and color fading after 3–4 years reduces the probability of observing these individuals if breeding in the Churchill study area. That two hatchlings were not detected in the local breeding population until the age of 8 years strongly suggests that some birds are temporarily leaving the population and then returning. In another study of this species on Akimiski Island, Nunavut, a breeding male underwent a long-distance (30 km) dispersal event. This also suggests, that despite generally greater nest site tenacity by males than females (Flynn et al. 1999, Lishman et al. in prep), males can and will disperse between breeding attempts in the same or different years. These difficult to document movements will continue to result in lower estimates of adult and juvenile survival for shorebirds breeding in mostly inaccessible habitats across the North American arctic, and reaffirm the importance of scale of the study area for documenting dispersal events (Greenwood and Harvey 1982, Jackson 1994, Sandercock and

Gratto-Trevor 1997, Colwell et al. 2007b, Stenzel et al. 2007).

Apparent survival estimates for philopatric individuals at intervals after the first return were high, and much higher than previous estimates from an adult sample from this population (Badzinski 2000; adult estimate of 0.71, CI: 0.64–0.78). Estimates of apparent survival for birds marked as adults may include first-time breeders of a wider range of ages that have lower survival rates. Alternatively, philopatric individuals may have higher site fidelity as adults than individuals that immigrate into our study sites as adults. Variation in individual strategies for space use have been reported for wintering Grey Plovers (*Pluvialis squatarola*), where individuals are either territorial or non-territorial, and do not change strategies during their lifetime (Turpie 1995). Our mean estimate of apparent adult survival is also higher than reported for the congeners Piping Plover (Larson et al. 2000, $s = 0.77$ for known-age juveniles), Snowy Plover ($s = 0.69$, Stenzel et al. 2007), and Kentish Plover ($s = 0.58$, Sandercock et al. 2005). Similarly, survival rates of known-age Pacific Golden Plovers (*Pluvialis fulva*; territorial: $s = 0.90$, non-territorial, $s = 0.82$) were 10–15% higher than those from a sample of unknown-age adults (territorial, $s = 0.80$, non-territorial, $s = 0.67$, Johnson et al. 2001). Variation in individual strategies for space use and apparent differences in age of first reproduction invite further research on the demography of short- versus long-distance migrant shorebirds to identify possible trade-offs in life history strategies, and to evaluate the consequences of life-history variation for planning conservation efforts.

ACKNOWLEDGMENTS

We thank the countless field assistants and students who helped band Semipalmated Plovers over the years. We also thank the Churchill Northern Studies Centre (CNSC) for their continued logistic and financial support. G. P. Kershaw kindly provided the map. The Science Horizons Youth Internship Programme of Environment Canada supported SW while the field work has been largely supported by NSERC grants to EN.

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BREEDING BIOLOGY AND NESTING SUCCESS OF THE SLATE-THROATED WHITESTART (*MYIOBORUS MINIATUS*) IN MONTEVERDE, COSTA RICA

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ABSTRACT.—I examined the breeding biology and nesting success of the Slate-throated Whitestart (*Myioborus miniatus*), a socially monogamous neotropical warbler, for five breeding seasons (2000–2004) in Monteverde, Costa Rica, near the center of its broad geographic range. Nesting was strongly seasonal, extending from late March through the end of June and coinciding with the end of the dry season and the onset of the rainy season in mid-May. Females constructed domed nests on open steep slopes or in banks along roads and trails. Mean clutch size was 2.9 eggs, and the mean incubation period was 14.2 days. Females performed all incubation of eggs and brooding of young nestlings, but both males and females fed nestlings and fledglings. Mean provisioning rate at nests when young were 5–9 days of age was 20.3 feedings/hr, and females fed young at a significantly higher rate than males (11.7 vs. 8.3 feedings/hr, respectively). Nestlings reached mean adult body mass of 9.5 g ~ day 7–8, and mean age at fledging was 11.3 days. Parents fed juveniles for at least 4 weeks after fledging; the latest record of adults feeding fledged young was for 40-day-old juveniles. Daily nest survival rates showed strong annual variation and generally declined as the nesting season progressed. Mean daily survival rate was 0.968 and estimated overall nest success was 40.3% with a mean of 2.6 young fledging from successful nests. Predation was implicated in ~85% of nest failures. *Received 17 February 2009. Accepted 22 July 2009.*

The genus *Myioborus* comprises 12 species of sexually monomorphic parulid warblers found in montane forests throughout the American tropics and subtropics (Curson et al. 1994). All members of the genus have contrasting black-and-white tails and animated foraging displays that function to startle potential insect prey, which are then pursued and captured in flight (Jabłoński 1999, Mumme 2002, Mumme et al. 2006). Species in the genus are termed "redstarts" by the AOU (1998) but "whitestarts" by the International Ornithological Congress Standing Committee on English Names (Gill et al. 2009). Recent phylogenetic analyses indicate that *Myioborus* is monophyletic (Pérez-Emán 2005) and part of a larger clade that includes five species from three additional genera: *Ergaticus* (2 species, Mexico and Guatemala), *Cardellina* (1 species, Mexico and the southwestern United States), and *Wilsonia* (2 species, northern United States and Canada) (Lovette and Bermingham 2002, Rabosky and Lovette 2008).

The Slate-throated Whitestart (*Myioborus miniatus*) is the most widely distributed *Myioborus* species, ranging from the mountains of northern Mexico to the southern Andes of Bolivia and northern Argentina (Ridgely and Tudor 1989, Curson et al. 1994, DiGiacomo 1995, McCormack et al. 2005). Genetic analysis suggests it is monophyletic, although populations from Mexico northwest of the Isthmus of Tehuantepec are genetically distinct from those in southern Mexico, Central America, and South America (Pérez-Emán 2005). In Central America, the Slate-throated Whitestart is monogamous, territorial, and often remains paired throughout the year (Skutch 1954, Shopland 1985). It occurs in mid-elevation montane forest throughout much of southern Central America and South America while a second species of *Myioborus* replaces it at higher elevation (Ridgely and Tudor 1989, Stiles and Skutch 1989, Curson et al. 1994).

In the last decade new data on the breeding biology, nest predation, and survival of tropical and southern hemisphere birds have fueled a vigorous resurgence of interest in avian life history evolution (e.g., Martin et al. 2000, 2007; Martin 2002, 2004; Ricklefs and Wikelski 2002). My objective is to contribute to this growing body of work by presenting data on the breeding biology and nesting success of the Slate-throated Whitestart in Monteverde, Costa Rica. Some data are available for this species from Guatemala, Costa Rica, and Venezuela (Skutch 1954, Shopland 1985, Collins and Ryan 1994), but I present a much more extensive analysis based on 5 years of study of a color-banded population and records from 132 separate nests.

METHODS

Study Area and Study Population.—The study was conducted during five consecutive nesting

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seasons (2000–2004) on a color-banded population of Slate-throated Whitestarts at the Estación Biológica Monteverde (EBM) and surrounding properties in Monteverde, Costa Rica (Nadkarni and Wheelwright 2000). The study area (10° 18′ N, 84° 48′ W) encompassed 35–45 breeding pairs of Slate-throated Whitestarts on territories established in primary premontane and lower montane wet forest (Haber 2000), old secondary forest, and abandoned pastures with scattered trees and shrubs at elevations of 1,400–1,700 m. Field work was conducted during January–June 2000, May–June 2001–2003, and April–June 2004.

I mist netted and color banded 170 adult Slate-throated Whitestarts during the study, either by attracting birds to song playback or by placing nets near active nests. An additional 172 individuals were color banded as nestlings. Gender of color-banded adults was assigned from either the presence of a brood patch in females or by subsequent behavioral observations, such as incubation or differences in vocal behavior; although both males and females produce song (Shopland 1985), males sing much more vigorously and frequently than females (Mumme 2002).

Data Collection.—Breeding territories were surveyed regularly to search for signs of nesting. The date of nest initiation (first egg date) was ascertained directly for nests found during building, but estimated indirectly for nests found with eggs or nestlings by extrapolating backwards using data on the laying sequence, incubation period, and growth and development of nestlings. Nests were usually checked every 3–4 days to ascertain nest fate, although a smaller sample of nests was checked once or twice daily at critical periods to obtain more detailed information about timing of egg laying, hatching, and fledging. I marked eggs daily as they were laid at seven nests and measured egg size with dial calipers. I used a 10-g or 30-g Pesola scale to measure body mass of nestlings at regular intervals from hatching (day 0) through day 8 at 11 nests where hatching date was known. Parental feeding rates at nests were calculated from data collected during 1- to 2-hr nest watches at 24 different nests where at least one member of the pair was color banded and the nests contained 2–3 nestlings that were 5–9 days of age. Nest watches were conducted from an observation blind during mid-morning to early afternoon (0800–1300 hrs) in dry weather. I recorded all feeding visits by males, females, and birds whose identity could not be ascertained. Nestlings were handled and color banded when 6–8 days of age at all nests. I made regular post-fledging visits to six territories where pairs nested successfully to record developmental state of juveniles and duration of post-fledging parental care.

Statistical Analysis.—Data on egg size were analyzed with a two-factor ANOVA in which nest and laying order were used as factors. Statistical comparisons of male and female provisioning rates at nests were made with a matched-pairs t test. Calculations for both tests were performed using R for Mac OS X (Version 2.8.1). Data on nestling growth were fitted to a third-order polynomial curve using Microsoft Excel 2004 for Mac OS X.

Daily Nest Survival and Nest Success.—I used the nest survival methods of Version 5.1 of Program MARK (White and Burnham 1999, Rotella 2008) to estimate daily survival rate (DSR) of Slate-throated Whitestart nests. The analysis was based on records from 128 nests where nest fate could be reliably ascertained. I evaluated a series of MARK nest survival models that used combinations of two categorical covariates, year (2001–2004) and nest habitat type (road banks, trail banks, and natural slopes), and two continuously varying covariates, date (calendar date within year) and nest age (number of days since first egg date). Covariates were coded and incorporated into models following Rotella (2008), allowing evaluation of models where nest DSR varied with year, nest habitat type, date, and nest age.

Candidate models were compared to the null model of constant nest DSR, S(.), based on Akaike's information criterion for small samples (AIC_c). The model with the lowest AIC_c value was considered to be the model that best fit the nest survival data, and Akaike weight (w_i) was used as a measure of the relative support for each candidate model (White and Burnham 1999). Estimates of DSR under specific models were obtained from model beta parameters and back transformation following Rotella (2008). I estimated the cumulative probability of overall nest success by raising DSR to the power 27.6, which is the mean duration of a successful nesting cycle in days.

RESULTS

Timing of Breeding.—Slate-throated Whitestarts in Monteverde have strong breeding seasonality. First egg dates ranged from 27 March to

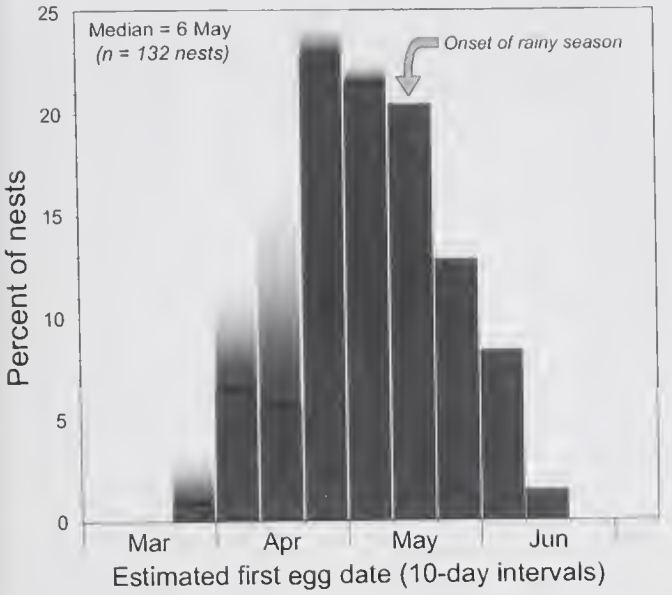


FIG. 1. Estimated first egg dates for 132 Slate-throated Whitestart nests in 2000–2004 in Monteverde, Costa Rica. Indistinct bars indicate that during 2001–2003 an unknown number of nests initiated in late March through early May either fledged young or failed before they could be discovered.

17 June with 6 May being the median date of nest initiation (Fig. 1). However, field work did not begin until after 10 May in 2001–2003, and several pairs had already fledged young from early nests. Thus, the true peak of nesting was likely earlier than 6 May (Fig. 1).

I found 132 nests during the study: 60 (45.5%) during building, 28 (21.2%) during egg laying or incubation, and 44 (33.3%) during the nestling stage. Pairs frequently renested when initial nesting attempts failed by making a second (n = 16; 12.1% of nests) or third (n = 1; 0.8% of nests) attempt. However, only one certain case of true double brooding was observed; in 2001, one pair was feeding fledged young from its first nest on 29 May and initiated a new nest on 31 May. The young from the second nest fledged successfully on 26 June.

Nest Building, Egg Laying and Incubation.—Slate-throated Whitestarts built domed nests in road banks (n = 70; 53.0%), trail banks (n = 19; 14.4%), or on steep slopes and natural banks in open areas such as pasture edges, ravines, washouts, and tree fall gaps (n = 43; 32.6%). Nests away from roads and trails were relatively more difficult to find, making it likely they were under-represented in the sample of 132 nests. I observed nest-building behavior for 31 pairs where at least one member of the pair was color banded and gender was known; in all 31 cases females alone carried nest material and constructed the nest. Males did not directly participate in nest building, but they frequently accompanied their mates to the nest during building.

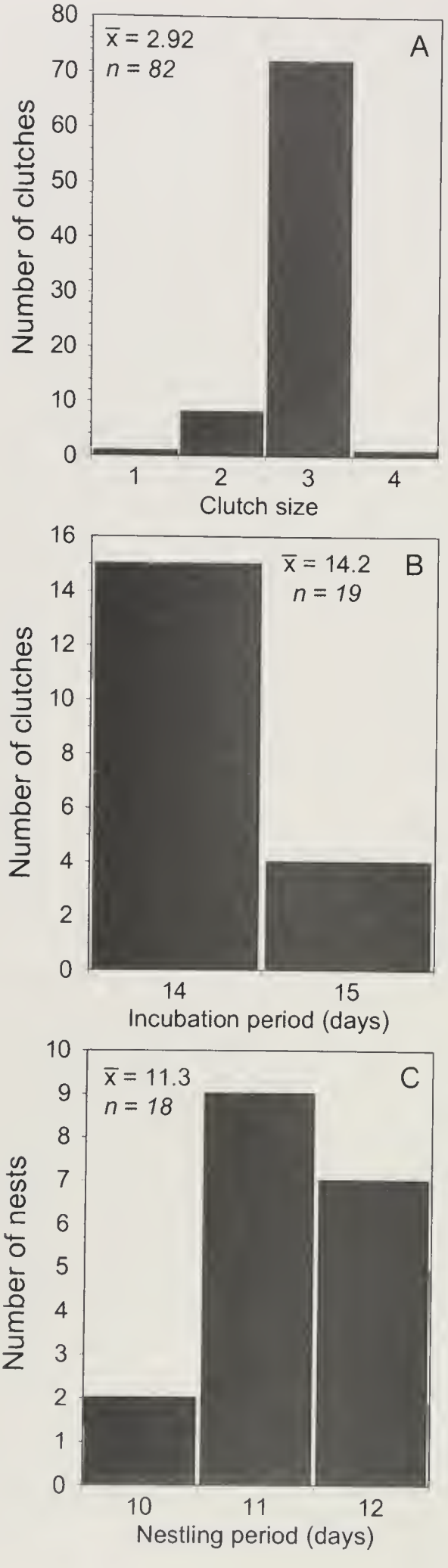
Clutch size was 1–4 eggs with a mean ± SE of 2.89 ± 0.04 (n = 82) and a strong modal clutch size of 3; 87.8% of nests contained three eggs (Fig. 2A). Laying occurred early in the morning, generally within 2 hrs of dawn. Eggs were laid on consecutive days in 13 (76.5%) of 17 nests where egg laying was monitored daily. Final clutch size was three eggs in all 13 of those nests. However, in four nests, a 1-day (n = 3) or 2-day (n = 1) gap occurred between laying of the first and second egg, and final clutch size was two eggs in three of the four nests. Thus, the mean ± SE interval between laying of the first egg and clutch completion was 2.12 ± 0.08 days (n = 17 nests).

Mean ± SE egg size in seven three-egg clutches was 16.67 ± 0.18 × 13.36 ± 0.07 mm (n = 21). Length and width varied significantly among nests (two-factor ANOVA $F_{6,12}$ = 26.71 and 9.29, respectively, both $P < 0.001$), but neither length nor width was significantly related to laying order (two-factor ANOVA $F_{2,12}$ = 0.50 and 0.19, respectively, both $P > 0.6$).

Females alone incubated the eggs, and the incubation period was 14–15 days (mean ± SE = 14.2 ± 0.1 days; Fig. 2B). Hatching was generally synchronous, and hatching success of eggs was high; of 160 eggs from 55 nests that survived through the end of incubation, 150 (93.8%) hatched.

Nestling and Fledgling Periods.—Nestlings averaged 1.4 ± 0.1 g (mean ± SE) at hatching (n = 3 nests) and reached mean adult body mass of 9.5 g ~ day 7–8 after hatching (Fig. 3). Both males and females provisioned nestlings, and female brooding of young nestlings ended when nestlings reached 5–6 days of age. Overall provisioning rates at nests with nestlings of age 5–9 days was 20.3 ± 1.0 feedings/hr (n = 24 nests); females provisioned young at a significantly higher rate (11.7 ± 0.8 feedings/hr) than males (8.3 ± 0.5 feedings/hr; two-tailed paired t test, t = 4.23, df = 23, $P < 0.001$).

Age at fledging was 11.3 ± 0.2 days (mean ± SE; Fig. 2C). Juveniles began to forage on their own by day 30, but parents continued to feed juveniles for at least 4 weeks after fledging; the latest record of adults feeding dependent young was of 40-day-old juveniles that had fledged 29 days earlier.



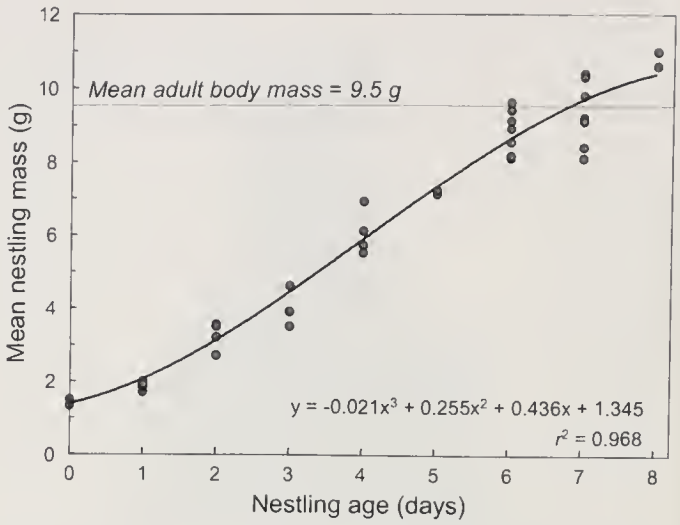


FIG. 3. Growth in body mass of nestling Slate-throated Whitestarts in 11 nests of known hateh date in Monteverde, Costa Riea, 2000–2003. Eaeh point represents the mean mass of nestlings from a single nest with either two or three young.

Daily Nest Survival and Nest Success.—Estimated nest daily survival rate (DSR) for the 128 nests used in the Program MARK analysis was 0.968 with a 95% confidence interval (CI) of 0.958–0.975. Estimated nest success, based on an average nest exposure period of 27.6 days (2.1 days between laying of the first egg and clutch completion, 14.2 days incubation, and 11.3 days during the nestling period), was 40.3% (95% CI, 30.5–49.9%). An average (± SE) of 2.61 ± 0.07 young fledged from 74 successful nests.

The MARK model of nest DSR that best fit the data included interaction terms between covariates year and date (Table 1). This model was 2.31 AIC_c units better than the second best model, which included the same two covariates in an additive model. These results suggest (1) there is considerable annual and seasonal variation in nest DSR, but (2) the precise nature of the seasonal effect of date is year-dependent. Estimated DSR varied annually from a low of 0.953 (95% CI, 0.927–0.970) in 2004 to a high of 0.989 (95% CI, 0.965–0.996) in 2003, corresponding to estimated nesting success of 26.3 and 72.7%, respectively (Fig. 4A). Nest DSR generally declined over the course of the nesting season, but the nature of the

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FIG. 2. Variation in clutch size (A), length of the incubation period (B), and nestling period (C) in Slate-throated Whitestarts in Monteverde, Costa Riea.

TABLE 1. Models of nest survival for 128 nests of Slate-throated Whitestarts in Monteverde, Costa Rica, 2000–2004, based on analysis with Program MARK. Models are ranked from best to least supported according to values of ΔAIC_c, the difference in Akaike's information criterion for small samples between the listed model and the top model. The covariates used in each model are shown in parentheses. Other columns show the number of parameters estimated in each model (K), model deviance, ΔAIC_c, and Akaike weight (w_i), a measure of the relative support for each model.

Model	K	Deviance	ΔAIC_c	w_i
S(year × date) – interaction	10	333.48	0.000	0.606
S(year + date) – additive	6	343.88	2.312	0.191
S(year)	5	347.89	4.307	0.070
S(date)	2	354.11	4.495	0.064
S(.) – constant survival	1	357.23	5.613	0.037
S(nest habitat type)	3	354.73	7.126	0.017
S(nest age)	2	356.94	7.326	0.016

seasonal decline varied from year to year (Fig. 4B). Neither nest site habitat type (road banks, trail banks, or natural slopes) nor nest age appeared to have a major influenee on DSR; models incorporating these eovariates reeeived little support and were ranked lower than the null model of eonstant DSR (Table 1). Thus, DSR appears to be largely independent of both nest site eharaeteristies and nest stage.

Apparent predation of the entire clutch (n = 19) or brood (n = 26) was the leading eause of nest failure, aecounting for 83.3% of all observed nest failures (n = 54). Abandonment of intact nests with eggs (n = 3) or young (n = 2) aeeounted for 9.3% of nest failures. An additional three nests (5.6% of failures) were abandoned after apparent partial nest predation redueed the nest eontents to either one egg (n = 2) or one nestling (n = 1). I also observed a single case of nest failure that may have been a result of male egg removal; at one nest where the banded male had disappeared and been replaeed by an unbanded immigrant, the three eggs were found intaet underneath the empty nest. The female was observed building a new nest with her new mate 6 days later.

DISCUSSION

Breeding Biology.—My results are generally eomparable to those of other studies of the breeding biology of the Slate-throated Whitestart and other *Myioborus* speeies. The Mareh–June breeding season coineiding with the end of the dry season and onset of the rainy season is consistent with the seasonality reported for Slate-throated Whitestarts in Costa Riea (Skutch 1954, Shopland 1985, Stiles and Skutch 1989) and Venezuela (Collins and Ryan 1994), and the Collared Whitestart (*M. torquatus*) at higher elevations in Monteverde (Shopland 1985). The Brown-capped Whitestart (*M. brunniceps*) in subtropical Argentina (26° S) is also strongly seasonal with a September-Deeember nesting season coineiding with a rainy season that begins in November (Auer et al. 2007). However, reeent work on the Speetaeled Whitestart (*M. melanocephalus*) suggests this speeies has a much more extended May-Deeember breeding season in Eeuador (00° 36′ S) that oecurs during relatively dry periods (Greeney et al. 2008).

Plaeement of Slate-throated Whitestart nests in banks along roads and trails, and on open steep slopes is eonsistent with other reports (Skutch 1954, Shopland 1985, Collins and Ryan 1994). Skutch (1954) reported the male partieipated in nest building at one of four nests where he observed nest eonstruction. In contrast, I observed nest building at 31 nests where at least one member of the pair was eolor banded and gender was known, and males did not carry nest material or assist in nest eonstruetion. Skuteh's report, however, is based on observations of unbanded birds, and he did not see both members of the pair arrive at the nest simultaneously with nest material. He wrote "I had proof that both birds worked at the nest, since I saw the seeond fly up to it with material in its bill, before the first, whieh had already added its contribution, had left the elearing" (Skuteh 1954:360). However, the ambiguities in his deseription, and the possibility the bird building the nest had slipped away unseen by Skuteh before returning with more nest material, suggest the possibility of nest eonstruction by males of this species should be viewed skeptieally until more persuasive evidenec is presented. Nest eonstruction in other species of *Myioborus* is either by the female alone or, in cases where gender eould not be ascertained, a single adult (Marshall and Balda 1974, Barber et al. 2000, Greeney et al. 2008).

The average cluteh size of 2.9 eggs is similar to that reported by others in Costa Rica (Skuteh 1954, 2.8 eggs, n = 11 nests; Shopland 1985, 2.8 eggs, n = 33 nests), but slightly higher than the mean elutch size of 2.4 eggs (n = 7 nests) reported for Slate-throated Whitestarts at

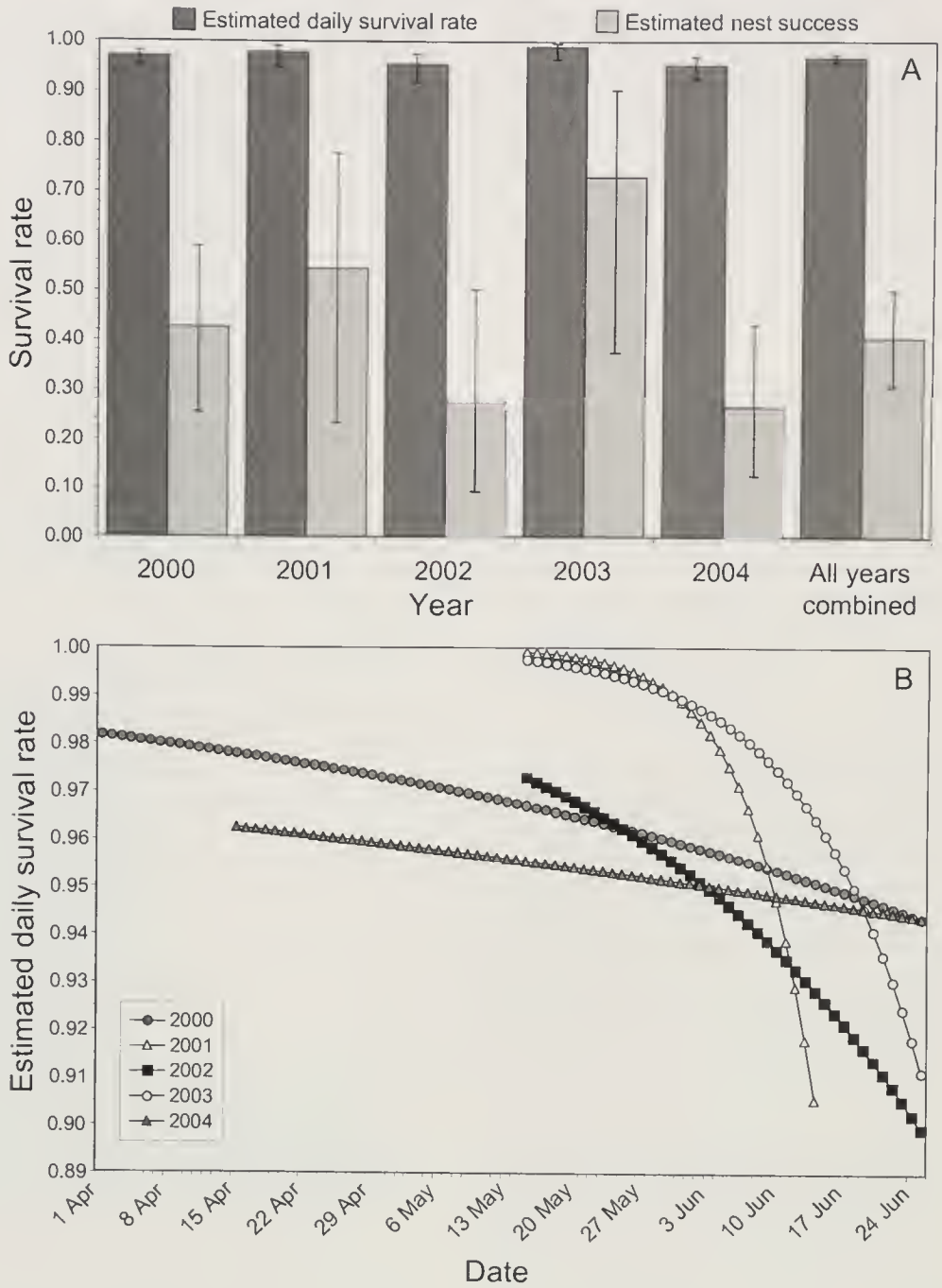

FIG. 4. Annual and seasonal variation in daily nest survival rate and overall nesting success of Slate-throated Whitestarts from Monteverde, Costa Rica, 2000–2004. (A). Annual variation in estimated daily survival rate and estimated nesting success. Mean ± 95% confidence intervals are shown. (B) The effect of date on predicted daily nest survival rates for 2000–2004, based on the most strongly supported model of nest survival, the S(year × date) interaction model (Table 1). Predicted daily survival rates are shown only for dates when active nests were being monitored.

10° 21′ N, 67° 41′ W in Venezuela (Collins and Ryan 1994). The clutch size of the congeneric Painted Whitestart (*M. pictus*) in the Chiricahua Mountains of Arizona is larger, averaging 3.1 eggs (Barber et al. 2000).

Mean egg size, 16.7 × 13.4 mm, was similar to that reported by Skutch (1954) (17.5 × 13.4 mm) and Collins and Ryan (1994) (16.3 × 12.3 mm). Egg size was not related to laying sequence, unlike many species of birds (e.g., Slagsvold et al. 1984, Lifjeld et al. 2005). Incubation periods of 13–15 days have been reported for Slate-throated Whitestarts in both Costa Rica (Skutch 1954) and Venezuela (Collins and Ryan 1994), but I observed incubation periods of 14–15 days. However, the mean incubation period I recorded in Monteverde, 14.2 days, is nearly identical to that reported by Skutch (1954) (14.4 days, $n = 5$ nests) and by Collins and Ryan (1994) (14.3 days, $n = 4$ nests).

The percentage of eggs surviving through the end of incubation that hatched successfully was 93.8%, relatively high for a tropical bird (Koenig

TABLE 2. Life-history traits of the Slate-throated Whitestart and three related north temperate zone warblers, the Red-faced Warbler, Canada Warbler, and Wilson's Warbler. The three related species were selected based on the phylogeny of Lovette and Bermingham (2002). Data for Slate-throated Whitestarts based on this study. Data for other species derived from Martin and Barber (1995), Conway (1999) and Ammon and Gilbert (1999).

Life-history trait	Slate-throated Whitestart	Red-faced Warbler	Canada Warbler	Wilson's Warbler
Breeding range	Tropical montane forest	Subtropical montane coniferous forest	Northern boreal forest	Northern boreal and humid Pacific forest
Nest site	Ground	Ground	Ground	Usually ground, some low in vegetation
Mean clutch size	2.9	4.2	4.3	3.9 (Pacific coast) 4.4 (NE US) 5.3 (Alaska)
Incubation period	14–15 days	13 days	11–12 days	11–12 days
Nestling period	10–12 days (mean 11.3 days)	11–13 days (mean 12 days)	10–11 days	10–11 days
Post-fledging dependence	29 days after fledging	No data	No data	24–25 days after fledging

1982). The low incidence of hatching failure at Monteverde, a montane cloud-forest site with cool ambient temperatures during the nesting season (Clark et al. 2000), is consistent with the hypothesis that one of the major causes of loss of egg viability and hatching failure is exposure to high ambient temperatures during the laying period (Stoleson and Beissinger 1999, Beissinger et al. 2005, Cooper et al. 2006).

Duration of the nestling period averaged 11.3 days, somewhat shorter than reported by Skutch (1954) (12.4 days, $n = 4$ nests) elsewhere in Costa Rica, but similar to that found for Monteverde by Shopland (1985) (11.7 days, $n = 16$ nests). The relatively greater role of females in feeding nestlings was also noted by Skutch (1954) at a nest of this species in Guatemala. Nestling growth appears to be slightly more rapid than that of Venezuelan nestlings (Collins and Ryan 1994), and the average provisioning rate I observed at nests (20.3/hr) is about twice the rate at which food is delivered to Brown-capped Whitestart nests in subtropical Argentina (Auer et al. 2007).

Few comparative data are available on duration of post-fledgling care of young, but both Skutch (1954) and Chipley (1976) noted the apparently long period of juvenile dependence by Slate-throated Whitestarts. My observation of adults feeding 40-day-old juveniles, 29 days after fledging is comparable to Shopland's (1985) observation of Collared Whitestarts feeding young 28 days after fledging.

Nesting Success.—Daily survival rate (DSR) of Slate-throated Whitestart nests in Monteverde was 0.968, yielding an estimated overall nesting success of 40.3%, comparable to the 45% nest success reported by Skutch (1954) for 11 nests. Data on overall nest DSR are not available for other species of *Myioborus*, but Auer et al. (2007) report the daily nest predation rate for Brown-capped Whitestarts in subtropical Argentina was 0.023. I found that ~85% of nest failure was due to predation, and the comparable figure of daily nest predation rate for Monteverde Slate-throated Whitestarts would be 0.028.

Two other studies of passerines in Monteverde have reported data on nest DSR and nesting success. Sargent (1993) found that nest DSR for Yellow-throated Euphonias (*Euphonia hirundinacea*), a species that nests in many of the same road banks favored by Slate-throated Whitestarts, was 0.972, yielding an estimated nest success of 33.6%. Nest DSR and estimated nesting success for cavity-nesting House Wrens (*Troglodytes aedon*) in Monteverde were considerably higher, 0.991 and 72.8%, respectively (Young 1994). My observed nest DSR of 0.968 in the Costa Rican highlands is greater than found in many studies of lowland neotropical birds (e.g., Robinson et al. 2000, Ryder et al. 2008) but comparable to an average nest DSR of 0.977 at 400 m elevation in Braulio Carrillo National Park, Costa Rica (Young et al. 2008).

Comparison to North Temperate Zone Warblers.—Recent phylogenetic analyses of the Parulidae and *Myioborus* (Lovette and Bermingham 2002, Pérez-Emán 2005, Rabosky and Lovette 2008) indicate the three North Temperate Zone warblers most closely related to the *Myioborus* whitestarts are Red-faced Warbler (*Cardellina*

rubrifrons), Wilson's Warbler (*Wilsonia pusilla*), and Canada Warbler (*W. canadensis*). Molecular evidence suggests the Hooded Warbler (*W. citrina*) is not part of the clade that includes *Myioborus* and the other *Wilsonia* (Rabosky and Lovette 2008).

The Slate-throated Whitestart in Monteverde, in contrast to its relatives in the North Temperate Zone, displays the standard suite of life-history traits—small clutch size, prolonged incubation, and perhaps prolonged nestling and post-fledging care (Table 2)—that characterize tropical birds (Martin 2004, Russell et al. 2004). Differences in duration of incubation are particularly striking, as the incubation period is 1–3 days longer for Slate-throated Whitestarts than for *Cardellina* or *Wilsonia* (Table 2). Recent studies have shown that longer incubation periods of tropical birds are at least partially a result of slower inherent developmental rate of eggs (Tieleman et al. 2004, Robinson et al. 2008), although proximate differences in nest attentiveness and incubation temperature may have a role as well (Martin et al. 2007). The nestling period of Slate-throated Whitestarts in Monteverde is only slightly longer than for *Wilsonia* and apparently shorter than for *Cardellina* (Table 2). It also appears to be slightly shorter than for other *Myioborus* whitestarts (Barber et al. 2000, Auer et al. 2007, Greeney et al. 2008). The relatively short nestling period in Monteverde merits further study, but may be affected by the relatively high rate at which food is delivered to nests (20.3 feedings/hr), the relatively rapid rate of nestling development, and the moderately high daily nest predation rate (0.028) (Martin et al. 2000).

Several studies have indicated the post-fledging period of juvenile dependence on parents is typically greater in tropical birds than in related temperate species (Skutch 1949, Russell et al. 2004, Tieleman et al. 2006). Data from Slate-throated Whitestarts are consistent with this hypothesis and suggest a slightly longer period of post-fledging care than for Wilson's Warbler (Table 2). However, additional data are needed to reach a firm conclusion about the relative duration of post-fledging parental care in *Myioborus* versus related temperate-zone warblers.

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BREEDING BIOLOGY OF KELP GULLS ON THE BRAZILIAN COAST

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ABSTRACT.—We studied clutch size, hatching and fledging success, and time necessary for chick Kelp Gulls (*Larus dominicanus*) to leave the nest throughout two breeding seasons (2004 and 2005) on Guararitama Island, São Paulo, Brazil. We followed 93 nests in 2004 and 97 nests in 2005. The average (± SD) clutch size was 2.09 ± 0.64 in 2004 and 1.93 ± 0.59 in 2005. Hatching success was 74% in 2004 and 53% in 2005, and fledging success was 54% in 2004 and 58% in 2005. Chicks grew quickly, following the linear equation $y(t) = 61g + 17.03g \times$ age (in days), and began to fly at 40 days.
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The Kelp Gull (*Larus dominicanus*) (Family Laridae) is widely distributed in the Southern Hemisphere, occurring in South America, South Africa, Australia, New Zealand, the sub-Antarctic islands, and the Antarctic Peninsula (Burger and Gochfeld 1996). It is a resident and common species in Brazil, occurring from Rio de Janeiro to the coast of Rio Grande do Sul (Sick 1997). This species usually establishes colonies with few to thousands of breeding pairs on islets and islands near the continent and on continental locations (Burger and Gochfeld 1996). Studies have reported a large increase in Kelp Gull populations in recent decades (Steele and Hockey 1989, Quintana and Yorio 1998). The Kelp Gull population at Peninsula Valdez, Argentina, increased from 3,200 to 6,500 pairs over a 10-year period (Quintana and Yorio 1998). This population growth has been attributed to enhanced post-fledging survival of juveniles due to the provision of supplementary food through anthropomorphic activities (Steele and Hockey 1989, 1991; Bertellotti and Yorio 1999).

Some authors believe gull population growth has been involved in displacement of other seabird species from breeding sites (Thomas 1972; Burger 1979, 1985; Quintana and Yorio 1998). Kelp Gulls have been observed to prey on eggs and chicks of Magellanic Penguin (*Spheniscus magellanicus*), Imperial Shag (*Leucocarbo atriceps*), Royal Tern (*Sterna maxima*), Cayenne Tern (*S. eurygnatha*) and Southern Giant Petrel (*Macronectes giganteus*) (Yorio et al. 1998). Effects of gulls on coastal wildlife are not confined to other seabirds. Thomas (1988) and Rowntree et al. (1998) observed Kelp Gulls injuring Right whales (*Eubalaena australis*) by picking off skin and fat when the whales emerge at the surface to breathe. These authors argue that intense harassment by gulls induces Right whales to abandon breeding areas before their young are sufficiently strong for the open sea.

Little is known about the breeding biology of the Kelp Gull despite its wide distribution and its great impact on other seabirds and mammals. (Crawford et al. 1982, Soares and Fonseca Schielfler 1995, Yorio et al. 1996, Yorio and Borboroglu 2002). Breeding biology studies are essential to understand the dynamics of a population, because changes in population size may result from processes of reproduction, survival, and migration (Doherty and Grubb 2002). Reproductive success is associated with several factors, including ecological conditions (intra- and inter-specific interactions, food availability, breeding site, etc.), and weather conditions (humidity, temperature, and wind) (Paynter 1949, Borboroglu and Yorio 2004). Studies that seek to understand long term survival and mortality rates in a population may be efficient for monitoring environmental change. An estimate of reproductive success is also essential for evaluating population growth. This information is needed to create future conservation programs for seabird communities.

We studied the breeding biology of the Kelp Gull on the south Brazilian coast. Our objectives were to: (1) measure the incubation period, (2) ascertain clutch size, (3) measure predation rate, (4) identify predators, (5) calculate the length of time required for chicks to become independent, and (6) measure the growth rate of chicks.

METHODS

Study Area.—Data were collected on Guararitama Islet, São Paulo, Brazil (24° 23′ S,

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46° 59′ W). This islet is 1.9 km from the continent and has an area of 1.2 ha with a rocky substrate, and shrub and grass-herb vegetation. Campos et al. (2004) estimated the *Larus dominicanus* population on Guararitama to be 100 breeding pairs.

Field Procedures.—We visited the islet every 5 to 7 days during 2004 and 2005 from the end of June to mid-November We recorded egg-laying dates, clutch sizes, egg measurements (length, width, and mass), chick measurements (mass, wing length, tarsus length, and beak length) and hatching dates. We measured eggs and chicks to the nearest 0.1 mm using calipers and to the nearest 1.0 g using a Pesola scale.

We marked all Kelp Gull nests on Guararitama Islet with satin tape. We marked eggs with a waterproof pen and chicks with satin tape, until they reached an appropriate size to receive a metal ring provided by CEMAVE/IBAMA (Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis). Nests were kept under surveillance throughout the breeding season to estimate survival, predation, and abandonment rates. A nest was considered active when it was well formed and contained eggs. It was considered to have been predated when broken eggs were found inside or near the nests, or when eggs disappeared without sign of hatching (e.g., excrement of the chicks). Nests were considered abandoned when eggs remained for 40 days without hatching. We defined hatching success as the number of chicks per eggs laid and fledging success as the number of chicks alive after 28 days per eggs laid (Mougeot and Bretagnolle 2006).

Statistical Analysis.—Egg volume was calculated following Hoyt (1979): $V = \text{length} \times \text{width}^2 \times 0.51$. We estimated the number of females by the number of breeding pairs (bx), assuming that each nest consisted of one pair. The estimated number of females was used to calculate fecundity (fx) and fertility (mx) (Pianka 2000):

bx = number of nests,

fx = number of eggs laid/number of females, and

mx = number of surviving eggs/number of females.

Two distinct peaks were observed in egg laying in 2004 and 2005. The 2004 breeding season was subdivided into an early and a later period, and the 2005 breeding season was divided into early, intermediate, and later periods, because the first peak was later in 2005. Differences within and between breeding seasons in egg volume and clutch size were evaluated with a *t*-test. Survival rates of offspring, hatching success, and fledging success were compared between breeding seasons using a χ^2 test.

Chicks captured on the day of hatching and at least one additional time during the breeding season ($n = 17$) were used to estimate the growth equation. We fitted the von Bertalanffy, Gompertz, and logistic three-parameter growth equations (Ricklefs 1967) to the data on chick mass using least squares procedures to analyze chick growth patterns. We analyzed the variance of the residuals distribution to identify which models best fit the data, and chose the model with low variance. We estimated the age of all other chicks captured only once during the breeding season based on the chosen growth equation. Growth curves that best fit the body size measurements (beak, tarsus, and wing length) were calculated using von Bertalanffy, Gompertz, and logistic three-parameter functions.

RESULTS

The Kelp Gull breeding season on Guararitama Islet began in mid-June and ended in early November. The first eggs were found on 24 June in 2004 and on 30 June in 2005. Egg laying continued until October with the last eggs being laid on 31 October in 2004 and 28 October in 2005. We recorded 195 eggs in 93 nests in 2004 and 172 eggs in 97 nests in 2005. Egg laying in both years showed two peaks during the breeding season. The first peak in 2004 occurred in July (93 eggs) and the second in September (102 eggs). The first peak in 2005 was in August (53 eggs) and the second in October (40 eggs) (Fig. 1).

Mean (± SD) clutch size was 2.09 ± 0.64 ($n = 93$) in 2004 and 1.93 ± 0.59 ($n = 97$) in 2005. The difference between the years was not significant ($t = 1.77$, $P = 0.07$). The average (± SD) incubation length was 24.12 ± 4.48 days in 2004 and 22.78 ± 3.27 days in 2005. The number of breeding females (bx) was 93 in 2004 and 97 in 2005. Fecundity (fx) was 2.096 in 2004 and 1.773 in 2005, and fertility (mx) was 1.387 in 2004 and 0.422 in 2005.

Estimated egg volume differed between the two peaks of each breeding season (2004: $t = 4.34$, $P < 0.001$; 2005: $t = 2.24$, $P = 0.026$). This difference cannot be attributed to the first peak consisting mainly of the first eggs laid by each

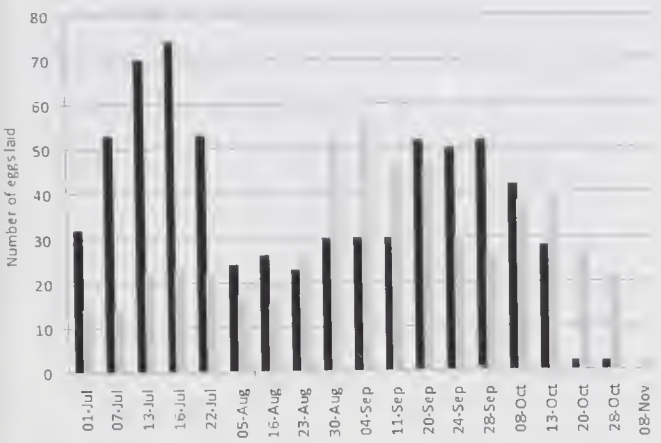

FIG. 1. Number of eggs laid throughout the Kelp Gull breeding season in 2004 (gray bar) and 2005 (black bar), on Guaraitama Islet, São Paulo, Brazil.

female, and the second peak consisting of the second and third eggs laid, because all eggs from the first peak hatched during the period of time between the peaks. The average volume of eggs laid during the first peak in 2004 was 88.11 ± 8.28 cm^3, while that of eggs laid during the second peak was 83.80 ± 12.68 cm^3. The average egg volume during the early period in 2005 was 87.01 ± 8.12 cm^3. The average egg volume during the first peak (intermediate period) was 87.18 ± 9.01 cm^3, and the average egg volume during the second peak (later period) was 82.43 ± 12.97 cm^3. The difference in egg volume between 2004 and 2005 was significant (t = 1.99, P = 0.046) with a mean (± SD) of 86.32 ± 10.37 cm^3 in 2004 and 84.13 ± 10.75 cm^3 in 2005 (Fig. 2).

The first peak of the season produced greater hatching success than the second peak in both years (2004: χ^2 = 10.09, P = 0.006; 2005: χ^2 = 7.11, P = 0.03) (Table 1). Hatching success was greater in 2004 than in 2005 (χ^2 = 18.13, P < 0.01) (Fig. 3). Predation was the principal cause of egg loss (25.6% in 2004 and 69.9% in 2005) and death of chicks (34.9% and 5.8%). The principal predators of Kelp Gulls were Black Vultures (*Coragyps atratus*) on eggs and adult Kelp Gulls on chicks.

Heat stress also affected loss of eggs and chicks. Air temperature can reach 33° C during the late breeding season in Guaraitama and, on hot days, the chicks appear lethargic and had difficulty breathing. Thus, they become easy prey for vultures and other raptors. Environmental data from Iguape Meteorological Station, Cptec/INPE, (www.cptec.inpe.br) for the breeding period indicated that 2005 was hotter than 2004, but the years did not differ in precipitation (temperature: t = 8.78, P = 0.000; precipitation: t = 0.53, P = 0.59).

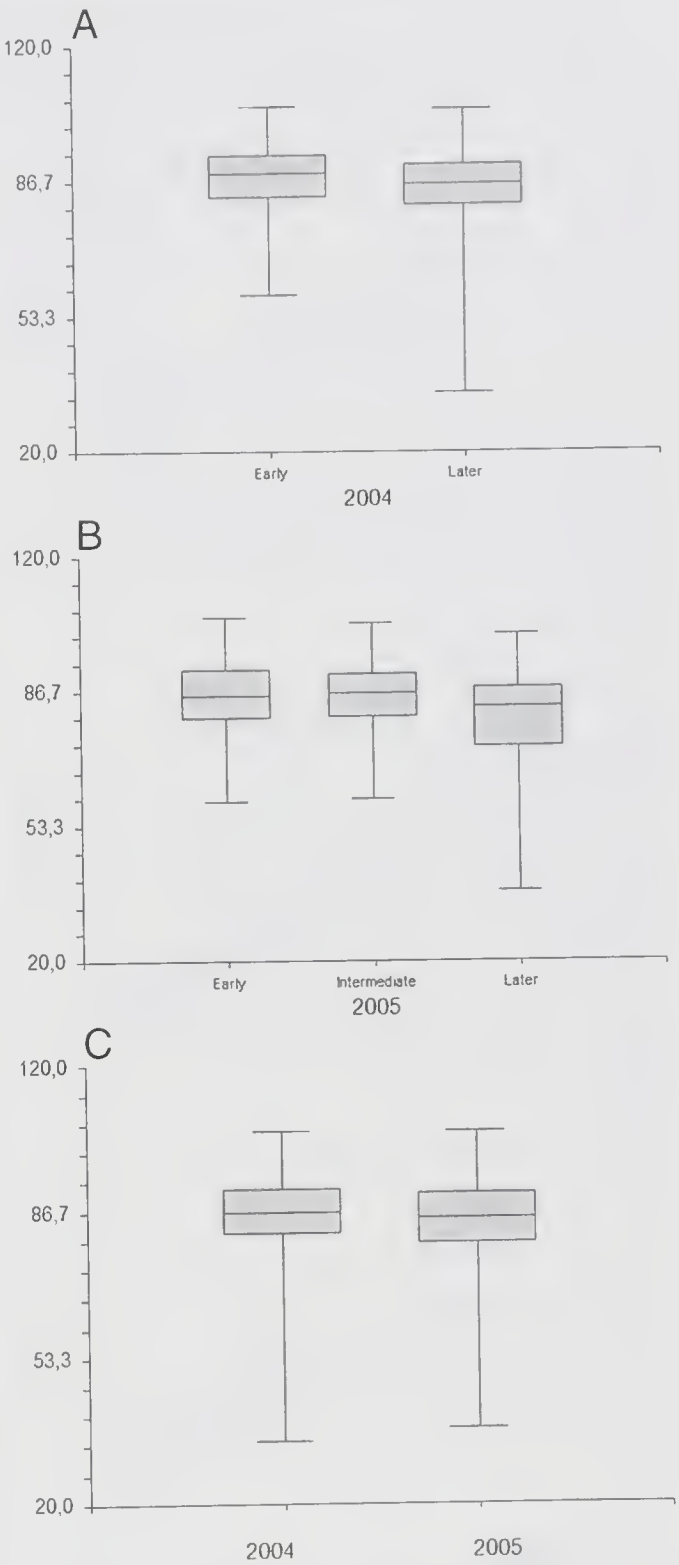

FIG. 2. Kelp Gull egg volume ($\bar{x}$ ± SD, cm^3) throughout the 2004 (A) and 2005 (B) breeding seasons and for both years (C), on Guaraitama Islet, São Paulo, Brazil.

Field observations indicated that chicks grew rapidly, remaining in the nest until they were 5 days of age. When chicks were 5 to 15 days of age, they moved around the island and become more visible to predators. Chicks were able to avoid predators after 30 days of age. They reached

TABLE 1. Hatching success rates throughout the breeding season of *Larus dominicanus* in 2004 and 2005, at Guaraitama Islet, São Paulo, Brazil.

Year	Period	Successful eggs	Predated eggs	Abandoned eggs	Totals
2004	Early	65 (69.9%)	16 (17.2%)	12 (12.9%)	93
	Later	64 (62.7%)	34 (33.3%)	4 (3.9%)	102
	Totals	129 (66.1%)	50 (25.6%)	16 (8.2%)	195
2005	Early	14 (35.9%)	23 (58.9%)	2 (5.1%)	39
	Intermediate	18 (20.0%)	69 (76.7%)	3 (3.3%)	90
	Later	9 (20.5%)	29 (65.9%)	6 (13.6%)	44
	Totals	41 (23. 7%)	121 (69.9%)	11 (6.4%)	173

an average mass and body size that made them difficult to catch by predators at this time. Chicks were flying at 40 days of age. The survival rate to fledging was 54% in 2004 and 58% in 2005 (X^2 = 1.79; P = 0.1798).

Three possible growth functions were compared (i.e., von Bertalanffy, Gompertz, and logistic functions). The variance of the residual distributions indicated the models did not differ significantly, and we present results only from the logistic equation. The logistic equation for body weight of 17 Kelp Gull chicks is weight (mass) = A/(1+B*EXP{−C*(days)}) (parameter values are in Table 2). We were able to predict the ages of chicks from their measured body mass using this curve. When chick mass increased linearly between 5 and 35 days of age, we derived a simplified formula: $y = y_0 + at$, where y_0 is birth mass (mean mass on day of hatching = 61 g); a is the estimated growth rate of 17.03 g/day, and t is age in days (Fig. 4). We observed rapid growth in all of the measured traits (beak, tarsus, and wing length) (Fig. 5). These measurements were fitted to growth models, and there were no significant differences among models (parameters estimated for the logistic three-parameter model, Table 2).

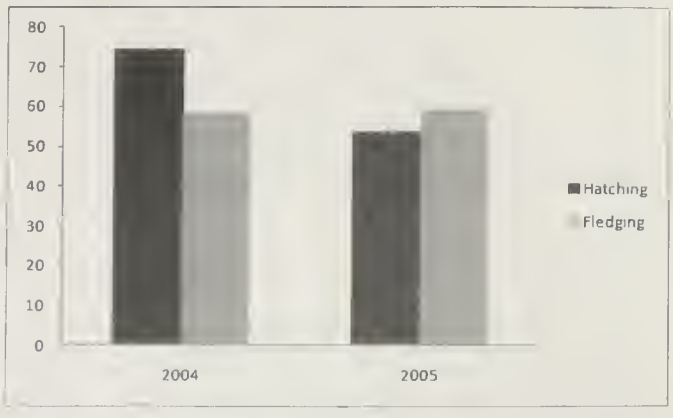

FIG. 3. Hatching and fledging success rates (%) of Kelp Gulls during the 2004 and 2005 breeding seasons, on Guaraitama Islet, São Paulo, Brazil.

DISCUSSION

The Kelp Gull breeding season on Guaraitama Islet was similar in both years, starting in mid-June and ending in early November. This same pattern was reported for the Santa Catarina coast in southern Brazil (Soares and Fonseca Schielfler 1995, Branco 2003), although Prellvitz et al. (2009) reported egg laying began on 1 June on Moleques do Sul, Santa Catarina. The Kelp Gull in Argentina reproduces from November to January in central and northern Patagonia (Borboroglu and Yorio 2004) and in mid-October in the Valdez Peninsula (Yorio and Borboroglu 2002). Yorio and Borboroglu (2002) report the Kelp Gull breeding season shows a direct relationship with latitude with gulls breeding earlier in more northern colonies. Laying stages may be related to latitude and to climatic conditions of the breeding localities (Fordham 1964).

Clutch size of Kelp Gulls on the Brazilian coast varies from one to three eggs. This clutch size has been reported for Kelp Gulls in Brazil, Argentina, and South Africa (Saliva and Burger 1989, Soares and Fonseca Schielfler 1995, Branco 2003, Borboroglu and Yorio 2004, Prellvitz et al. 2009), and for other species of *Larus* in temperate regions (Paynter 1949, Kadlec and Drury 1968). The average clutch size in our study (2.09 in 2005

TABLE 2. Logistic growth model parameters. A = asymptotic growth rate; B = constant integration growth; C = growth rate of Kelp Gull chicks (n = 17), at Guaraitama Islet, São Paulo, Brazil.

	A	B	C
Body mass, g	1,165.34	14.25	0.11
Wing length, mm	135.30	4.86	9.41
Tarsus length, mm	77.88	1.78	0.06
Beak length, mm	47.63	1.41	5.69

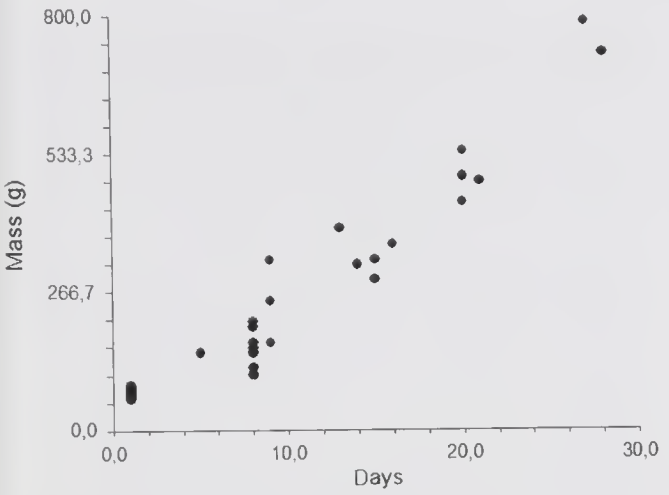

FIG. 4. Growth (mass) of Kelp Gull chicks on Guararitama Islet, São Paulo, Brazil.

and 1.95 in 2005) is comparable to that of other studies in Patagonia, Argentina (2.3–2.5 eggs, Yorio and Borboroglu 2002), southern Brazil (2.3 eggs, Soares and Fonseca Schielfler 1995; 1.98–2.26 eggs, Branco 2003; 1.97 eggs, Prellvitz et al. 2009), and the Antarctic Peninsula (2.5 eggs, Fraser 1989). There were two peaks of egg laying at Guararitama Islet in both years. However, Yorio and Borboroglu (2002) in Argentina and Saliva and Burger (1989) in South Africa observed only one laying peak for Kelp Gulls. We believe the bimodal egg laying at Guararitama Islet may be a consequence of environmental conditions, including temperature and humidity. Prellvitz et al. (2008) reported Kelp Gull colonies are smaller in warmer and less productive waters, suggesting that environmental conditions can influence size and reproductive success of colonies.

Egg size is related to the ability of the female to obtain food resources throughout the laying period (Herbert and Barclay 1988). We observed significant differences in egg volume between the two laying peaks during each breeding season (Fig. 2). Females produced larger eggs during the early period than during the later period. Skórka et al. (2005) have shown that food availability is reduced late in the breeding season. Thus, older pairs breeding early in the season are expected to have better success/survival than younger pairs due to greater experience and provisioning skills. Additionally, smaller average egg volume was observed in 2005 than in 2004 ($t = 1.99$; $P = 0.046$). These differences may reflect environmental changes that influence chick survival.

The optimal temperature for bird embryo development is 37–38° C; temperatures above

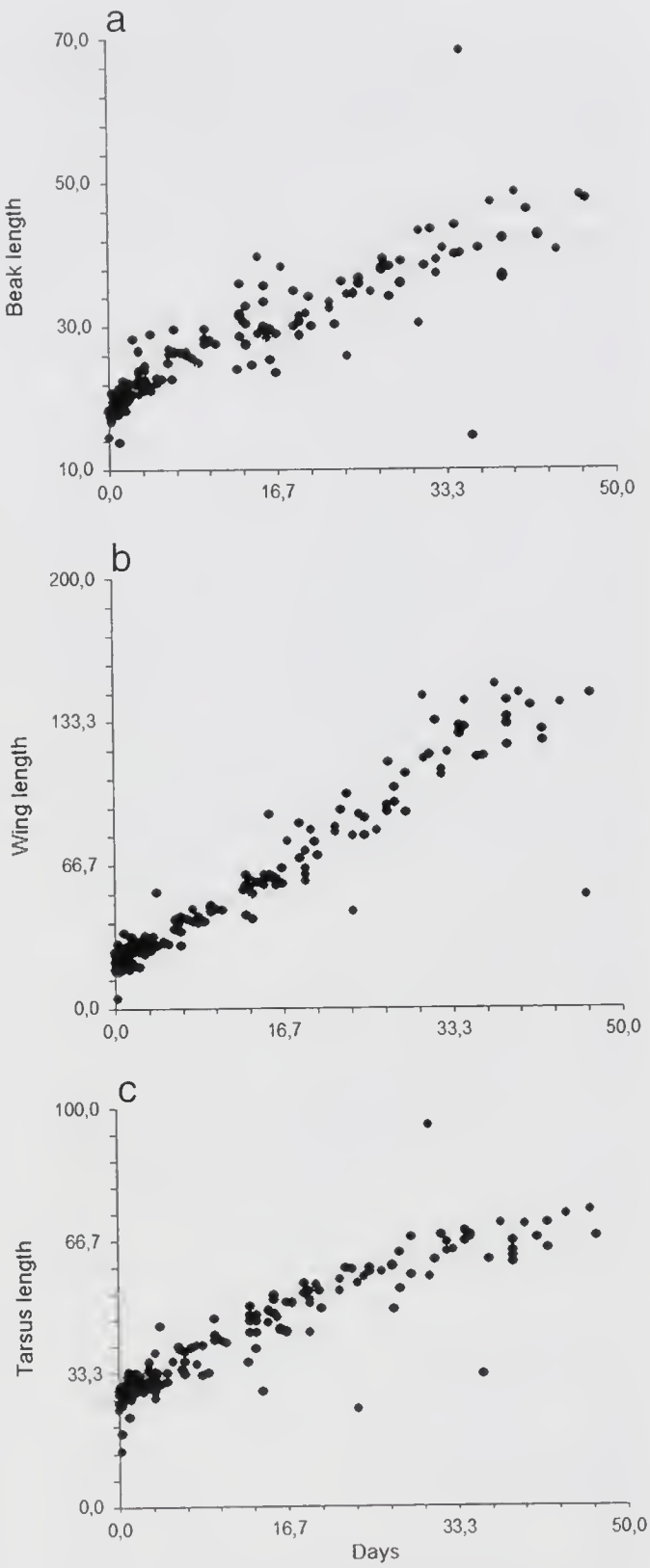

FIG. 5. Growth (tarsus, wing, beak length) of Kelp Gull chicks on Guararitama Islet, São Paulo, Brazil, during the 2004 and 2005 breeding seasons.

40.5° C are deadly (Gill 1994). The air temperature during the 2004 breeding season ranged from 17° to 36° C, and during 2005 from 17.5° to 40° C (Iguape Meteorological Station). Borboroglu and Yorio (2004) reported the breeding season of Kelp Gulls at Isla Vernacci, southwest-

ern Argentina, ends in the middle of January, when the temperature reaches 40° C. By that time, the chicks are already flying. Salzman (1982) reported that temperatures above 32° C are harmful to chicks of *Larus occidentalis*, often causing death. Salzman (1982) reported that stress caused by excessive heat is one of the main causes for egg loss and chick mortality.

The high mortality observed in 2005 may have been due to high temperatures recorded throughout the breeding season, which left nests exposed to predators. The principal cause of egg loss (25.6% in 2004, 69.9% in 2005) at Guararitama was predation by vultures, while the principal cause of chick mortality (34.9% in 2004, 25.0% in 2005) was predation by adult Kelp Gulls. Borboroglu and Yorio (2004) reported egg loss of 28% and chick morality of 50%. These authors also reported chick predation by adults of the same species. They believe that chick predation by adults of the same species occurs when chicks invade breeding territories, searching for shade and protection under vegetation. Predation can be reduced by parental care and by selection of a more hidden site for nest building (Borboroglu and Yorio 2004).

Other predators observed to prey on eggs and chicks of Kelp Gulls includes Subantartic Skuas (*Stercorarius antarcticus*) and Southern Crested Caracara (*Caracara plancus*) (Yorio et al. 1995, Sick 1997, Yorio and Borboroglu 2002). However, Prellvitz et al. (2009) observed parental negligence and starvation to be the main mortality factor for eggs and chick Kelp Gulls, respectively, on Deserta Island. The number of eggs abandoned and chick death by starvation was small (<5%) in our study. Pierotti and Bellrose (1986) reported that high losses from parental negligence or egg fertility could indicate lower food availability or inferior food quality. Prellvitz et al. (2009) reported 51% hatching success on Deserta Island, similar to that in 2005 on Guararitama Islet. However, hatching success on Guararitama in 2004 was 74%, similar to that reported by Yorio and Borboroglu (2002) at Peninsula Valdez, Argentina. These differences may be related to environmental variability in temperature and humidity. Stable years can have great hatching and fledging success and hotter years can result in great mortality from predation or starvation.

Kelp Gull chicks grow rapidly and this species displays parental care during incubation and feeding of chicks. Borboroglu and Yorio (2004) reported that parental care gradually decreases over the breeding season, increasing predation risk. Kelp Gull chicks start to move around the island after 5 days of age. This movement, when they are only a few days of age, seems to be a behavioral characteristic (Yorio et al. 1996). Chicks weigh 800 g at 35 days and are already flying. Capture by predators at this phase is difficult. Yorio and Borboroglu (2002) also observed rapid growth of chick Kelp Gulls in colonies on the coast of Argentina. Prellvitz et al. (2009) reported that most chick mortality on Deserta Island, Brazil, occurred in the first week of life. This rapid growth rate may represent an evolutionary adaptation for escape from predators.

Kelp Gulls breed on the Brazilian coast during the winter, probably to avoid higher summer temperatures and to seek better conditions for embryo development. Individuals that breed early in the season have an advantage over pairs breeding later in the season. The main predators of eggs and chick Kelp Gulls are Black Vultures, whose impact is greatest at the egg stage, and adult Kelp Gulls, which prey on young chicks. Chicks have rapid growth, probably as a means of avoiding predators. Despite the high predation rate observed in 2005 (a hotter year), Kelp Gulls had a high survival rate (54% in 2004 and 58% in 2005). If these chicks survive to the reproductive stage, this suggests an incremental population growth rate of 50% each year. This population growth may pose a serious problem for the conservation of other seabirds.

ACKNOWLEDGMENTS

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COOPERATIVE BREEDING OF THE SOCIETY KINGFISHER (*TODIRAMPHUS VENERATUS*)

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ABSTRACT.—We present evidence of cooperative breeding in Society Kingfishers (*Todiramphus veneratus*). Groups of three kingfishers were observed cooperatively excavating nest cavities, incubating, and provisioning young. Three bird groups also comprised half of visual observations recorded during island-wide point transect surveys that occurred during the onset of breeding. Society Kingfisher densities were an order of magnitude greater than other Pacific kingfisher populations, which may lead to resource saturation and evolution of cooperation in this species. Our results lend insight into cooperative behaviors and facilitate conservation of birds in French Polynesia. *Received 30 July 2009. Accepted 12 October 2009.*

Cooperative breeding has been a focus of behavioral ecologists and evolutionary biologists for decades (Skutch 1935, Brown 1987, Stacey and Koenig 1990, Koenig and Dickinson 2004). Broadly defined, cooperation occurs when more than two individuals contribute to a single brood (Cockburn 2004, 2006). A range of social structures are considered to be cooperative (e.g., Stacy and Koenig 1990), and they occur in taxa as diverse as ants (Order Hymenoptera; Reeve and Ratnieks 1993) and hawks (e.g., *Buteo galapagoensis*; Faaborg and Bednarz 1990). Cooperative breeding among birds can include multiple parents that lay eggs in a single nest (*Crotophaga sulcirostris*; Vehrencamp 1978), large breeding collectives that include multiple breeding pairs and numerous non-breeding individuals (*Melanerpes formicivorous*; Koenig et al. 1995), or colony-nesting species with helpers assisting related clans (*Merops bullockoides*; Emlen and Wrege 1989). Cooperation appears to be most commonly exhibited as groups comprised of parents and offspring that work together to rear related young (e.g., *Picoides borealis*; Walters 1990). This behavior is rare, as ~2.5% of birds are considered to be cooperative breeders (Brown 1987).

Several life history characteristics are commonly associated with cooperative breeding (Du Plessis et al. 1995). Some cooperatively breeding birds are year-round territorial species with young that have extended parental dependence (Brown 1987, Stacey and Koenig 1990). Cooperation can also occur in situations with limitations in breeding resources or territories, in which potential dispersers are considered to be ecologically constrained from breeding independently (Selander 1971, Brown 1974, Gaston 1978, Stacey 1979, Emlen 1982). This concept was first presented as *habitat saturation* (Brown 1974) and later articulated as the *ecological constraints hypothesis* (Emlen 1982). A conceptual model of the hypothesis was described as a situation in which all available habitats already host territories that are maximally compressed in size (Brown 1987). Alternatively, some suggested that cooperation must have originated on the natal territory, and that potential dispersers delayed dispersing because the *benefits of philopatry* outweighed those of immediate dispersal (Stacey and Ligon 1987, 1991).

We present the first observations of cooperative breeding by the Society Kingfisher (*Todiramphus veneratus*). The Society Kingfisher is a member of a genus that includes 11 imperiled species (near threatened or above, IUCN 2008) of the 21 recognized (Clements 2007). We present three lines of evidence for cooperation in the Society Kingfisher. First, we describe direct observations of helping behaviors at nests. Second, we report observations of cooperative groups of birds throughout the study area and during the breeding season. Finally, we provide population density estimates and compare those to densities reported for other Pacific *Todiramphus* species to illustrate the potential for habitat saturation.

METHODS

We observed Society Kingfishers on the island of Moorea (17° 32′ S, 149° 50′ W) during surveys

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FIG. 1. Copulation with three Society Kingfishers present on 31 December 2008 on the island of Moorea, French Polynesia. (Photograph by T. Ghestemme.)

and visits in November and December 2008, and January 2009. We described cooperative behaviors observed on two territories during nest excavation, incubation, and brood rearing phases (17° 32′ 11″ S, 149° 49′ 46″ W; and 17° 32′ 26″ S, 149° 47′ 20′ W). Each observation period lasted ~30 min, and dates and times associated with each behavior are reported.

We conducted variable distance point-transect surveys (Buckland et al. 1993) of Moorea's landbirds at 46 stations in undeveloped upland forests. Stations were separated by 200 m. The distance was estimated to all landbirds detected by visual or auditory means during a 10-min observation period at each station. We also recorded the number of kingfishers present when detected outside of prescribed observation periods. Point-transect data were analyzed with Program DISTANCE (Thomas et al. 2006) to estimate the density of Society Kingfishers on the island of Moorea. We pooled observations into 25-m groups and conducted the analysis with a half-normal key, truncation at 100 m, and default model selection adjustment routine (Akaike's Information Criteria; AIC_c; Burnham and Anderson 2002). Limited detections reduced potential adjustment parameters to two, but the results were intuitively appealing and Chi-square goodness of fit tests indicated the approach was reasonable ($\chi^2 = 3.66$, df = 2, $P = 0.16$).

RESULTS

On 25 (1510–1612 hrs), 26 (1045–1125 hrs), and 27 (0720–0815 hrs) November 2008 we observed three Society Kingfishers cooperatively excavating nest cavities in the central and southeastern regions of Moorea. Three kingfishers were perched in close proximity (<2 m) on each occasion. All group members flew to the trees (*Neonauclea fosteri*) of interest and struck the main stem with their beaks. Nest excavation was accompanied by loud calling, and quieter growling and warbling vocalizations typical of Pacific kingfishers. Two individuals consistently perched closer together (within 50 cm) and struck the cavity more often than the third bird, which only struck the tree once during each observation period. Two birds were observed excavating a cavity without a third individual present on two other territories. On 31 December (0925 hrs), two birds copulated (Fig. 1) while the third bird passively perched within 10 cm. No aggressive behaviors were observed during nest excavations or copulations. Two of three group members were

marked with individual-specific combinations of colored plastic leg bands on 13 January 2009 on the central region territory. On 13 (1040–1125 hrs), 14 (1500–1630 hrs), and 15 (1600–1715 hrs) January, at least three birds (2 color banded and 1 unbanded) were observed entering the nest cavity and incubating. The same 2 color-banded and 1 unbanded group members were also observed delivering food items to the nest on 19 February (0630–0830 hrs).

Observations of three-bird groups of Society Kingfishers throughout the island of Moorea provided further support for cooperation. Kingfishers were detected at 61% of the point-transect stations during island-wide surveys. Of the birds visually observed, we encountered seven three-bird groups and seven two-bird groups. Three-bird groups were observed on an additional four territories outside of survey periods. The distance-based analyses indicated densities of 2.4 kingfishers/ha (95% CI = 1.6–3.5). These results suggest Society Kingfisher territories on Moorea were 0.82 ha (95% CI = 0.57–1.19) in size for pairs or 1.23 ha (95% CI = 0.85–1.90) for trios, based on multiplying density estimates by group size. No groups were observed with more than three individuals.

DISCUSSION

Our observations of cooperative nest excavations and food delivery by Society Kingfishers are congruent with cooperative behaviors reported for other birds, and we suggest the species qualifies as a cooperative breeder. Cooperative breeding has been described in other *Todiramphus* kingfishers of Pacific Oceania. Beckon (1987) reported three-bird nest excavation by Collared Kingfishers (*T. chloris*), and substantial work was directed at cooperative behaviors of Micronesian Kingfishers (*T. cinnamominus*) (Kesler and Haig 2005, 2007a). This behavior is relatively common among other Coraciiformes. Cooperative breeding has been documented for Rufous Hornbills (*Buceros hydrocorax*) (Witmer 1993), White-fronted Bee-eaters (*Merops bullockoides*) (Emlen and Wrege 1989), Laughing Kookaburras (*Dacelo novaeguineae*) (Legge and Cockburn 2000), and Pied Kingfishers (*Ceryle rudis*) (Reyer 1980) among others.

Our distance-based results indicated a Society Kingfisher population density that was higher than for other Pacific kingfisher species in similarly structured habitats. Mean territory size was 5.9 ha for cooperatively breeding Micronesian Kingfishers (Kesler and Haig 2007b, c) and 6–10 ha for Tuamotu Kingfishers (*Todiramphus gambieri*; Coulombe and Kesler, in prep). Kingfishers exclude neighboring conspecifics from their territories, and territory sizes translate to population densities of 0.5 Micronesian Kingfishers/ha (assuming territories with 3 birds), and 0.2 Tuamotu Kingfishers/ha (assuming a breeding pair). Our results indicate population densities of Society Kingfishers on Moorea that are 4.4 times higher than cooperatively breeding Micronesian Kingfishers and 6.7 times higher than breeding pairs of Tuamotu Kingfishers. This high density of Society Kingfishers on Moorea may overwhelm breeding resources, saturate habitats with territories, and lead to the ecological constraints previously suggested to cause cooperation in other species (Emlen 1982, Walters et al. 1992).

Cooperative breeders provide opportunities to simultaneously test fundamental theories in behavioral ecology and conservation biology because both management and cooperative breeding theory often focus on limited resources (Walters et al. 1992, Komdeur 1994). For example, much has been learned about conservation and evolution of cooperative sociality in the endangered Red-cockaded Woodpecker (*Picoides borealis*) (Connor et al. 2001). Conservation managers in French Polynesia should consider the importance of identifying and managing limited kingfisher resources to maintain robust populations. Cooperative breeding also has the potential to influence population resilience by creating a reserve set of adult helpers that are poised to breed when opportunities are presented, which can buffer the effects of environmental or demographic stochasticity (Walters et al. 2002, Kesler and Haig 2007a).

Society Kingfishers were abundant in the undisturbed upland forests of Moorea and Tahiti (Gouni and Zysman 2007), and it is somewhat striking that cooperative behaviors were not previously described. A similar lack of knowledge persists for many Pacific birds despite the immense contributions that island species have made to biological understanding. We advocate for added focus on the basic natural history of birds in remote and threatened regions, including the islands of Pacific Oceania.

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REPRODUCTIVE SUCCESS OF BURROWING OWLS IN URBAN AND GRASSLAND HABITATS IN SOUTHERN NEW MEXICO

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ABSTRACT.—We examined Burrowing Owl (*Athene cunicuaria*) reproductive success at 144 nests in urban (n = 80) and grassland (n = 64) habitats in southern New Mexico in 2000 and 2001. Nest success was higher in grassland compared to urban areas (81 vs. 68%) but urban landscapes fledged more young per successful nest (3.85 vs. 3.07). Mean fledging success per nest was similar between habitats with 2.60 and 2.50 fledglings in urban and grassland habitats, respectively. Fledging success was categorized as failure, low, and high. Reproductive success in both habitats was associated with measures of owl density. High success in urban landscapes was associated with fewer surrounding nests, an index of larger nesting territories, and open space. Failure was associated with solitary nests. This suggests owls benefit from the presence of other nesting pairs as long as the density is not too high. High success in grassland habitats was associated with fewer surrounding nests, index of larger nesting territories, edge nests, and lower fledgling success of the nearest nest. Higher nest success, but fewer fledglings per successful nest, suggests competition for resources in this habitat. *Received 23 February 2009. Accepted 30 September 2009.*

Few native species are as widely distributed and appear as adaptable to environmental change as Burrowing Owls (*Athene cunicularia*). This species ranges throughout much of North, Central, and South America, and the West Indies (Haug et al. 1993, Desmond et al. 2001). Most research, however, has focused on the western subspecies (*A. c. hypugaea*), which is distributed across western North America. The western Burrowing Owl is associated with fossorial mammals and historically occurred across grasslands, desert scrub, and sagebrush (*Artemisia* spp.) habitats (Haug et al. 1993, DeSante et al. 2004). More recently, they have occupied urban and agricultural landscapes, often occurring at densities substantially higher than observed in native habitats (Millsap and Bear 2000, DeSante et al. 2004, Rosenberg and Haley 2004).

Populations of the western Burrowing Owl are declining in many parts of their range despite the wide distribution and flexibility of the species to occupy a variety of burrow systems and habitat types (Sheffield 1997, Holroyd et al. 2001). Long-term Breeding Bird Survey data (1966–2007) indicates an annual decline in Burrowing Owl populations of 4.4% in the northern and central plains states compared to an annual increase of 1.5% in the southern plains states (Sauer et al. 2007). Causes of declines are many but are thought to be mainly attributed to habitat loss and degradation. Land conversion, including loss of grasslands and populations of prairie dogs (*Cynomys* spp.), likely is involved. Land conversion may also be contributing to an apparent shift in owl populations to urban and agricultural landscapes, particularly in the southern part of their range (DeSante et al. 2004, Rosenberg and Haley 2004, Conway et al. 2006; but see Poulin et al. 2005). The Imperial Valley of California, prior to agriculture, had low densities of Burrowing Owls, but now supports among the densest known populations of this species (DeSante et al. 2004).

Studies in urban environments in Florida have linked Burrowing Owl density and reproductive success with low and moderate levels of development (Millsap and Bear 2000). Once development exceeded 60% of an area, Millsap and Bear (2000) found owl populations and reproductive success declined, likely due to increased human disturbance. Benefits of sodded, landscaped lawns and parks in urban environments include increased availability of insects and lizards, due to regular watering and lawn maintenance (Wesemann and Rowe 1987), and birds (Mrykalo et al. 2009). Negative effects include increased predator densities, disturbance, and road fatalities (Wesemann and Rowe 1987, Millsap and Bear 2000).

A comparison of reproductive biology between native and urban habitats will help identify management needs for owls in both habitats, but particularly urban environments. Burrowing Owl populations in native habitats across the Great Plains are most commonly linked to black-tailed prairie dog (*Cynomys ludovicianus*) colo-

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nies (Haug et al. 1993, Desmond et al. 2000, Orth and Kennedy 2001, Griebel and Savidge 2007). Reproductive success in the Great Plains was positively associated with density of fossorial rodents (black-tailed prairie dogs; Desmond et al. 2000, Lantz et al. 2006) and was both positively and negatively associated with measures of owl density (Desmond et al. 2000, Griebel and Savidge 2007). This suggests that Burrowing Owls may benefit from prairie dog presence (or other fossorial rodents) through the dilution effect or by cueing in on alarm calls and the presence of other owls by alerting each other to predators.

Increased Burrowing Owl populations in urban landscapes underscore the importance of identifying threats and conservation needs for urban populations. A number of studies have examined Burrowing Owls in different systems including comparative studies in urban and agricultural systems (Conway et al. 2006), but there is a lack of comparative studies on owl reproduction in urban and native environments. Burrowing Owls nesting in urban compared to rural environments in west Texas exhibited greater vigilance (Chipman 2006). Serious concern has been raised about the sustainability of owl populations in urban and agricultural environments due to conflicts with human activities, especially changes in land management (DeSante et al. 2004, Rosenberg and Haley 2004). Major threats in Las Cruces, New Mexico are construction and land management activities, maintenance of irrigation canals and fields, use of recreational fields with large audiences on weekends and evenings, nests in areas of high pedestrian traffic, and vehicle mortalities. We hypothesized that nest site characteristics and reproduction would differ between urban and grassland sites due to different predation pressure, disturbance, and resource availability in these two environments. Prairie dog colonies are larger in area, contain higher burrow densities and, although dynamic, are more stable compared to rock squirrel (*Spermophilus variegatus*) colonies. We predicted fledging success would be higher in grasslands due to decreased levels of human disturbance, lower rates of predation, and benefits from higher densities and larger areas of colonial sciurids. Owls may benefit from the presence of prairie dogs through the dilution effect and by cueing in on prairie dog alarm calls (Desmond et al. 2000).

METHODS

Study Area.—Research was conducted in urban (n = 19) and grassland (n = 7) habitats of the northern Chihuahuan Desert in southern New Mexico, USA in two adjacent counties, Doña Ana and Sierra. Urban nests were monitored within a 4,533-ha area of Las Cruces (human population 74,267; U.S. Census Bureau 2000). Nests in grassland habitats were on the 145,750-ha Armendaris Ranch within the Pedro Armendariz Land Grant, 122 km north of Las Cruces. Average annual rainfall for southern New Mexico is 24.7 cm with greater than 56% in June–September (Western Regional Climate Center Desert Research Institute 2002). Annual rainfall in 2000 was 1.6 cm above average in Las Cruces (10.1 cm above average for the May–Jul nesting period) and 5.6 cm below average on the Armendaris Ranch (average during the May–Jul nesting period). The following year was drier with annual precipitation 10.2 and 9.9 cm below average for urban and grassland sites, respectively, and 1.2 and 3.3 cm below average for the May–July nesting period.

Dominant vegetation in the Las Cruces area consisted of honey mesquite (*Prosopis glandulosa*), desert globemallow (*Sphaeralcea coccinea*), snakeweed (*Gutierrezia* spp.), manicured lawns, ornamental trees and shrubs, and flood-irrigated agricultural row crops. Average elevation of the study area was 1,358 m. Burrowing Owl nests in Las Cruces were mainly associated with rock squirrel burrows; owls were also nesting in cavities excavated by pocket gophers (*Geomys* spp.) as well as human-made (drain pipes) and artificial burrows. The city of Las Cruces Community Development Department made the following distinctions concerning land use: developed land consisted of residential, office, commercial, industrial, and community; open space included agricultural fields, parks, arroyos, and vacant lots. Nesting owls occurred in all of these areas.

Dominant vegetation on and surrounding prairie dog colonies at the Armendaris Ranch included alkali sacaton (*Sporobulus airoides*), tobosa (*Pleuraphis mutica*), burrograss (*Scleropogon brevifolius*), three-awn (*Aristida* spp.), black grama (*Bouteloua eriopoda*), honey mesquite, creosote (*Larrea tridentata*), cholla (*Opuntia imbricate*), and yucca (*Yucca* spp.). Elevation at the seven colonies on the Armendaris Ranch was

1,386 m. Cattle were removed from the Armendaris Ranch in 1993 and replaced with 1,200 head of bison (*Bison bison*) (Hartsough 2002). Burrowing Owl nests on the Armendaris Ranch were in black-tailed prairie dog colonies averaging 4.5 ha (range 1.7–10.4 ha) re-established within 6 years prior to the initiation of this study. Historically, black-tailed prairie dogs were likely important for Burrowing Owls in southern New Mexico; prairie dogs were extirpated from most of the region and are now reduced to a few areas (Oakes 2000).

Data Collection.—Searches for nesting owls occurred once each week beginning 1 March 2000 and 1 February 2001. Urban areas were searched by visiting known nesting locations obtained from local contacts, searching historic locations, and visiting known rock squirrel colonies. All suitable habitat and burrows within each location were searched for nesting owls. Re-established prairie dog colonies on the Armendaris Ranch were searched for owls by walking transects through colonies and examining each burrow (Desmond et al. 2000). Nests were identified based on presence of a nesting pair on ≥1 occasion and the presence of shredded grass and scat at the burrow entrance (Garcia and Conway 2009). Indications of nest initiation in urban areas also included shredded paper, plastic, and aluminum foil. The surrounding area was thoroughly and repeatedly searched for other nesting pairs when a nest was located.

Nests were monitored weekly (0500–1200 and 1630–2130 hrs) until nesting attempts were terminated or young fledged. Time spent at each location, 15–60 min, depended on our ability to obtain reliable above-ground brood counts. Each brood was counted twice a week for 60 min at dawn (0500–0800 hrs) and dusk (1830–2100 hrs) to identify the size of the initial brood. A reliable count was considered to be verification of each brood member. The site was revisited at dawn or just prior to dusk within the week to recount the number of young, if all juvenile owls were not accounted for within 60 min. This method is more intensive than the standardized 20 min counts recommended by Gorman et al. (2003), and provides a reliable estimate of the number of young. Nest success data were limited to nests initiated before 30 May to avoid including re-nesting attempts in the data set. Fledging success was defined as the number of young per nest attempt surviving until 42 days of age, the age when juveniles are capable of extended flight (Haug and Oliphant 1990, Desmond et al. 2000). A successful nest was defined as one that fledged a minimum of one chick. The rate of nest success for each year was defined as the number of successful nests divided by the total number of attempts within each of the two study areas.

Characteristics quantified around nest sites included number of breeding pairs within a 75-m radius of each nest, distance to the nearest-neighboring nest, fledging success of the nearest-neighboring nest, burrow type, number of satellite burrows within a 50-m radius of each nest, distance to the nearest perch used by adult males and, for urban nests, the category of urbanization (developed vs. open space). We chose to count nests within a 75-m radius of the nest burrow due to observations that chicks will venture up to 75-m from the nest burrow before fledging (Desmond and Savidge 1999, Desmond et al. 2000). We also recorded for the 2001 field season whether a nest burrow was new or had been used as an owl nest the previous season.

Statistical Analyses.—A paired-samples *t*-test was used to compare the mean number of nests per site between years for each habitat. Distance to the nearest-neighboring nest, number of nests within a 75-m radius, number of satellite burrows within a 50-m radius, number of nests per ha, and perch distance were also compared between habitat types, pooling years, and within habitat types between years, using Student's *t*-test for two independent samples. The number of fledglings per nest attempt was not normally distributed and could not be corrected using log or square-root transformations. Thus, nests were separated into three categories of fledging success and a Chi-square test for homogeneity was used to test for differences between habitat types in fledging success categories: failure (0 fledglings), low success (1–2 fledglings), and high success (≥3 fledglings). These categories were used to decrease variability while maintaining the structure of the relationship between the outcome and the predictor variables (Hosmer and Lemeshow 2000).

We used multinomial logistic regression to evaluate variables as predictors of Burrowing Owl fledging success categories for each habitat type. Data within habitat types (grassland vs. urban) were combined for the 2 years, and regression analysis was conducted separately for each habitat type. We developed a set of candidate *a priori* models for each habitat type that we believed would be the most biologically meaningful, 16 for

TABLE 1. Habitat variables (mean ± SE) and *t* statistics for Burrowing Owl nest sites in urban (Las Cruces) and grassland (Armendaris Ranch) habitats pooled for 2000 and 2001 in southern New Mexico.

Sites	Nest site variables				
Urban vs. grassland		Urban	Grassland	t_{141}	P
	Nearest-neighbor distance, m	159.1 ± 11.7	49.7 ± 6.3	7.66	<0.001
	# Nests within 75 m	0.8 ± 0.1	3.6 ± 0.3	−8.99	<0.001
	Nest density/ha	0.13 ± 0.01	1.58 ± 0.10	−14.12	<0.001
	# Satellite burrows	10.7 ± 1.3	44.3 ± 2.4	−13.14	<0.001
	Perch distance, m	184.0 ± 56.3	27.9 ± 3.4	2.46	0.015
Grassland by year		2000	2001	t_{61}	P
	Nearest-neighbor distance, m	45.0 ± 7.6	52.2 ± 9.1	−0.54	0.589
	# Nests within 75 m	2.8 ± 0.5	4.0 ± 0.4	1.81	0.093
	Nest density/ha	1.6 ± 0.1	1.9 ± 0.1	−3.78	<0.001
	# Satellite burrows	38.2 ± 4.4	47.6 ± 2.6	−1.93	0.058
	Perch distance, m	31.4 ± 7.6	26.0 ± 3.2	0.76	0.451

grassland and 18 for urban habitats. We used a balanced combination of the same five variables for each habitat type (year, number of nests within a 75-m radius of each nest, fledging success of the nearest neighboring nest, number of satellite burrows within a 50-m radius of each nest, and distance to nearest perch) but added one additional variable, category of urbanization, to the urban data set. The city of Las Cruces makes multiple distinctions concerning land use, but to increase the number of nests within a land-use group, we limited land use to two categories: open space (including agricultural fields, parks, arroyos, and vacant lots) and developed land (including residential, commercial, and community lands). We calculated Akaike's Information Criterion (AIC) corrected for small sample size (AIC_c) for each model using SYSTAT 12.0 (Systat 2007). All models were ranked according to ΔAIC_c and models with a $\Delta AIC_c \leq 2$ were considered competing models (Burnham and Andersen 2002). Model weights were calculated for each model and cumulative weights for all variables were calculated. All variables were evaluated for pairwise collinearity using Pearson Correlation. None of the variables included in either sets of models was considered collinear (variables correlated < 0.70).

A Chi-square homogeneity test was used to evaluate whether a burrow was more likely to be re-used if the nest had been successful the previous year. A Mann Whitney *U* test was used to compare fledgling success between new nest burrows and burrows that were re-used as nests from the previous year. All statistical analyses were performed using SYSTAT, Version 12.0 (Systat 2007).

RESULTS

Sixty-six nests were located and monitored in 2000, 43 within 19 urban sites and 23 within six prairie dog colonies. Seventy-eight nests were located in 2001, 37 within 15 urban sites and 41 within seven prairie dog colonies, including one newly established colony. There was no difference in the mean number of nests per site in urban areas between years ($P = 0.470$), but the number of nests established within the original six prairie dog colonies in grassland habitats was greater in 2001 ($t_{11} = -3.72$, $P = 0.003$). In urban areas, 75% of nests were associated with rock squirrel systems. All monitored nests in grassland areas on the Armendaris Ranch were associated with black-tailed prairie dog colonies.

Site characteristics and owl population dynamics differed between the two habitats (Table 1). Mean nearest-neighbor nest distances in grasslands were significantly closer, and the mean number of nests within 75 m and nest densities were both significantly greater compared to urban sites (Table 1). The mean number of satellite burrows within a 50 m-radius of the nest was significantly higher, whereas mean perch distance of the adult male from the nest burrow was significantly less in grassland compared to urban habitats (Table 1).

Grassland site characteristics exhibited differences between years. The number of nests in prairie dog colonies almost doubled the second year and, predictably, nest density was greater in

TABLE 2. Burrowing Owl nest success in urban and grassland habitats in southern New Mexico pooled for 2000 and 2001. Percent reproductive effort within three fledging success categories (failure, low success, high success) was examined using a Chi-square test for homogeneity (X^2 = 5.59, df = 2, P = 0.061). Fledging data were not normally distributed.

Productivity parameters	Urban	Grassland
% Failure[a] (n)	32.5 (26)	18.8 (12)
% Low success[b] (n)	16.5 (13)	28.0 (18)
% High success[c] (n)	51.0 (41)	53.0 (34)
Totals	100 (80)	100 (64)
Successful nests[d] (% ± SE)	54 (67.5 ± 5.6)	52 (81.3 ± 4.8)
Young fledged	208	160
Fledglings/attempt ($\bar{x}$ ± SE)	2.6 ± 0.25	2.5 ± 0.22
Fledglings/successful nest ($\bar{x}$ ± SE)	3.9 ± 0.22	3.1 ± 0.20

[a] Failure = 0 fledglings.
[b] Low success = 1–2 fledglings.
[c] High success = 3+ fledglings.
[d] Successful nests = ≥1 chick.

2001 (Table 1). However, no difference was detected in the mean number of nests within a 75-m radius of a nest, mean nearest-neighbor distance, or mean perch distance from the nest between years (Table 1). The mean number of satellite burrows within a 50-m radius of a nest in 2001 was higher (Table 1). No differences (P > 0.05) in site characteristics were observed between years in urban landscapes.

No differences were detected among the three reproductive success categories between habitat types (X^2 = 5.59, df = 2, P = 0.061); however, there was a tendency for higher nest failure in urban (32.5%) compared to grassland (18.8%) habitats, but more nests in the low-success category for grassland compared to urban sites (28 vs. 16.5%; Table 2). Sixty-eight percent of Burrowing Owl pairs nesting in urban areas compared to 81% in grassland habitats successfully fledged at least one chick (Table 2). The mean number of young fledged per successful nest was 3.85 and 3.07 for urban and grassland sites, respectively. On average, nests in urban and grassland areas fledged 2.60 and 2.50 young per nest attempt, respectively (Table 2).

Differences were detected in variables influencing fledging success between the two habitats. The global model containing all five variables in grassland habitats had overwhelming support (Table 3). This was the only competing model for grassland sites with a model weight of 0.99. Higher success was associated with nests having fewer satellite burrows within a 50-m radius (40 vs. 57), greater perch distance from the nest (34 vs. 19 m), and lower fledging success of the nearest Burrowing Owl nest (2.40 vs. 3.60 fledglings), as compared with failure. Owls with low success had a greater number of owl nests within a 75-m radius (5.60 compared to 2.70) when compared with high success owls. A year effect was also observed, as significantly more nests were in the low success category the second year (Table 3). Cumulative model weights supported the importance of all five variables (Table 4).

The two top models in urban habitats were competing models; variables included in the top model were number of nests within a 75-m radius, perch distance, and number of satellite burrows

TABLE 3. Top three multinomial logistic regression models for each habitat type ranked in order of increasing ΔAIC_c influencing Burrowing Owl fledging success in urban and grassland habitats in southern New Mexico in 2000 and 2001. + (or −) on a predictor variable indicates increased (or decreased) probability of high-success vs. failure or high success vs. low success as the predictor variable increases for the two multinomial submodels.

Habitat	Models	High vs. failure	High vs. low success	K	AIC_c	ΔAIC_c	w_i
Grassland							
1.	NEST, PERCH, NNFS, SAT, YR	+NEST, −PERCH, +NNFS, +SAT, +YR	+NEST, −PERCH, −NNFS, −SAT, −YR	5	98.94	0	0.99
2.	NEST, PERCH, SAT	+NEST, −PERCH, +SAT	+NEST, −PERCH, −SAT	3	107.86	8.92	0.01
3.	NEST, NNFS, SAT	+NEST, +SAT, +NNFS	+NEST, −SAT, −NNFS	3	112.26	13.32	0
Urban							
1.	NEST, PERCH, SAT	−NEST, −PERCH, +SAT	+NEST, −PERCH, +SAT	3	157.03	0	0.44
2.	NEST, SAT, URB	−NEST, +SAT, +URB	+NEST, −SAT, +URB	3	158.63	1.60	0.20
3.	NEST	−NEST	+NEST	3	160.36	3.33	0.08

TABLE 4. Cumulative model weights of variables in *a priori* multinomial logistic regression models used to identify habitat characteristics that predicted Burrowing Owl fledging success in grassland and urban environments in southern New Mexico for 2000 and 2001.

Habitat	Variable (j)	w + (j)
Grassland	Year	0.99
	Nests	1.00
	NNFS	0.99
	Satellites	1.00
	Perch distance	0.99
Urban	Year	0.18
	Nests	0.89
	NNFS	0.17
	Satellites	0.73
	Perch distance	0.61
	Urbanization	0.36

within 50-m of each nest. The second ranking model contained the number of nests within a 75-m radius, number of satellite burrows within a 50-m radius, and measure of urbanization (Table 3). Nests in the high success category, as compared to failed nests, had fewer nests within a 75-m radius (0.40 vs. 0.80) and nests in open space had higher success than nests in developed areas (Table 3). The number of satellite burrows was retained in both models with a higher number associated with high versus low success. Perch distance was retained in one of the top two models with greater perch distance associated with high success compared to low success and failure. Cumulative model weights supported the number of nests within a 75-m radius, number of satellite burrows within a 50-m radius, and perch distance as strongly influencing fledging success; number of nests negatively, and number of satellite burrows and perch distance positively influenced productivity (Table 4).

Owls in urban areas in 2001 re-used 51.4% of nest burrows from the previous year whereas in prairie dog colonies 22.0% of the nest burrows were re-used. There was no significant relationship between burrow re-use and previous nest success ($P > 0.05$). There was also no relationship between burrow re-use and nest success in urban environments ($P = 0.373$), but there was a tendency for owls in grasslands occupying a burrow used the previous year to produce more fledglings than new nest burrows ($U = 90$, $P = 0.072$).

DISCUSSION

Burrowing Owl nest densities were approximately one order of magnitude greater in prairie dog colonies than in urban areas. The majority of nests in urban areas were associated with rock squirrel burrows, which resemble prairie dog colonies as both provide multiple nesting opportunities. However, rock squirrel colonies are smaller, more ephemeral, and may be in open rocky areas, flat terrain, irrigation canals, embankments, or among rock piles (Findley 1987). Prairie dog colonies are larger, provide more nesting opportunities, have higher burrow densities, occur in grasslands, and are more stable (King 1955). Prairie dog colonies had a greater number and density of burrows, covered substantially more area compared to rock squirrel colonies, and were surrounded by more foraging habitat.

Owls nesting in urban environments maintained nearest neighbor distances ($\bar{X} \pm$ SE = 159 $\pm$ 12 m) similar to other studies in urban and agricultural systems (Rosenberg and Haley 2004) whereas spacing of nests in prairie dog colonies in our study was closer ($\bar{X} \pm$ SE = 50 $\pm$ 6 m) than commonly observed in this system (Desmond et al. 1995, Griebel and Savidge 2007). However, available data supports closer spacing in prairie dog colonies for southern sites (Ross 1974, McNicoll 2005, Teaschner 2005), possibly attributable to fewer and smaller colonies resulting in fewer suitable nesting sites. This is supported by the rapid occupancy of small colonies ($\bar{X} \pm$ SE = 4.85 $\pm$ 1.33 ha) on our study area by Burrowing Owls immediately following establishment (T. E. Waddell, pers. comm.).

Fledging success did not differ between the two habitat types as predicted but was low in comparison to average clutch sizes for Burrowing Owls (7–9 eggs; Haug et al. 1993) and reproductive performance from several other studies (Coulombe 1971; Martin 1973; Botelho and Arrowood 1998; Lutz and Plumpton 1999; MJD, unpubl. data). Different mechanisms appeared to be influencing the low productivity at these sites. Sixty-eight percent of all nest failures in our study occurred in urban sites; nests in these sites tended to either fail or be highly successful. In comparison, grassland sites had lower rates of failure but produced fewer young per successful nest. Higher nest failure in urban areas suggests higher rates of

nest predation and/or abandonment in this environment, whereas fewer fledglings per successful nest in grasslands suggest increased competition for resources. We were not, however, able to differentiate between predation and nest abandonment. Owls in west Texas experienced higher rates of disturbance in urban compared to rural environments (Chipman 2006), but it was not known if this influenced productivity. Foraging data from this study suggested that owls in urban environments may have higher foraging rates possibly compensating for increased disturbance. Studies in Canada (Wellicome 2005) and California (Haley 2002), using food supplementation, found that Burrowing Owls were food-limited during the nestling period. York et al. (2002) attributed low reproductive success of Burrowing Owls in the Imperial Valley of California to the lower amounts of vertebrate prey in their diets compared to other studies. Fledging rates in grassland habitats appeared to be negatively impacted by the high density of owls in these small, recently established colonies. This was most apparent in 2001 when number of nests in prairie dog colonies almost doubled, resulting in a higher density of nesting owls compared to the previous year.

Measures of Burrowing Owl density appeared to strongly influence productivity at both sites but for different reasons. Productivity in our grassland habitats was strongly negatively impacted by measures of nest/owl density resulting in fewer fledglings per successful nest. This suggests that competition for resources and/or aggressive interactions were factors in this environment. Griebel and Savidge (2007) in South Dakota reported higher productivity for nests that were further from the nearest neighboring nest. The higher success of nests with fewer satellite burrows in our study was associated with nests along colony edges, suggesting that reproductive success was higher for edge nests. Several studies have suggested that Burrowing Owls prefer to nest near colony edges (Eckstein 1999, Desmond et al. 2000, Orth and Kennedy 2001). Possible advantages include reduced competition related to fewer surrounding nests and easier access to off-colony foraging. Perching distance is an indication of the territory size surrounding the nest burrow and sentinel owls closer to the actual nest likely had smaller territories and increased competitive interactions. Owl proximity to the nest may also increase nest vulnerability to predation; however, predation rates in the incubation and early nestling stage for this habitat type were low (81% of nests were successful). Nest failure rates were higher in urban habitats where owls perched further from the nest. The combination of increased owl densities and below normal precipitation in grassland habitats in 2001 likely contributed to increased competition for fewer resources on those sites. Our results from grassland habitats support the need for larger prairie dog colonies in the southern plains that have experienced greater fragmentation compared to northern populations (Miller et al. 1994). Desmond et al. (1995) found that Burrowing Owls in prairie dog colonies exhibited clustered distributions with greater inter-nest distance when colonies were $\geq$35 ha, and were randomly distributed with smaller inter-nest distances in colonies $<$35 ha. These data suggest owls require larger colonies to exhibit preferred nest spacing, and our results indicate that closer nest spacing negatively impacts productivity.

Nest density in urban areas also appeared to have the strongest impact on reproduction. Nests in the high success category were associated with lower densities of nesting owls compared to the low success category, suggesting competition for resources also influenced reproduction at these sites. However, failed nests had the lowest nest density and tended to be solitary, suggesting the presence of other nesting pairs may increase productivity, possibly through increased predator detection, as long as sufficient space is available to reduce competition for nearby resources. Most unsuccessful nests failed during the incubation or early nestling stages, suggesting nest abandonment or predation. Increased development in Florida resulted in reduced owl densities despite higher prey populations in these environments (Millsap and Bear 2000).

The loss of suitable burrows and space for multiple nesting pairs may increase predation risk for owls nesting in developed areas. Productivity in urban environments in our study was also associated with land use practices with high nest success associated with open space compared to developed areas. Open space is associated with larger habitat patches that provide more nesting opportunities and may have lower predation pressure and less disturbance (vehicular or pedestrian traffic). Density of some of the major urban predators, including domestic cats (*Felis catus*) and common raccoons (*Procyon lotor*) are

likely higher in residential areas; we observed owls mobbing domestic cats at urban sites on several occasions. As Burrowing Owls become increasingly associated with urban environments, city planning offices should work with local and state biologists to identify and preserve areas important to Burrowing Owls. This should include identifying areas free from disturbance with sufficient space for multiple nesting pairs, preservation and management of fossorial rodent populations associated with Burrowing Owls, and installing and maintaining artificial nest burrows when necessary.

Owls in urban habitats re-used significantly more nest burrows than those in grassland sites. Two factors likely contributed: burrow availability and resident owls. Fewer suitable burrows were available to owls in urban compared to grassland habitats. Holmes et al. (2003) reported re-use rates in Oregon ranging from 57 to 87% where owls primarily nest in American badger (*Taxidea taxus*) burrows. They attributed high re-use rates to a shortage of suitable burrows, especially in sandy soils. Fewer burrows are available in rock squirrel colonies, and rock squirrel populations in urban areas are often eradicated due to conflict with human activities. A portion of our urban owl population was resident year-round (27% of urban owls in 2001 were present the first week in Feb). Burrowing Owls in a mainly resident population in California had 85% nest site fidelity (Rosenberg and Haley 2004). The combination of a partially year-round resident population and fewer suitable nest burrows in urban compared to grassland habitats likely contributed to a higher re-use rate in urban environments.

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DIETARY TRENDS OF BARN OWLS IN AN AGRICULTURAL ECOSYSTEM IN NORTHERN UTAH

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ABSTRACT.—Barn Owl (*Tyto alba*) diets were studied for 15 years in Utah. Ninety-eight percent of 111,016 prey items were mammals, heavily dominated by voles (*Microtus* spp.). Food-niche breadth (FNB) was 3.33 for the entire sample and varied gradually but significantly among the 15 years and among seasons. Frequency of prey in the diet did not vary significantly from year to year or among seasons. Mean daily temperatures did not vary significantly among years but annual precipitation totals and days when deep snow covered the ground varied significantly among years. Irrigation for agriculture may have partially mitigated annual precipitation fluctuations. Hay, one of the most important crops on the study area, increased over the study period and other crops decreased slightly in the amount planted. Hectares of hay planted, hectares of corn planted, and hectares of barley planted were the variables that combined to best predict annual FNB. *Received 9 February 2009. Accepted 31 July 2009.*

Long-term studies can reveal how variation in prey populations, climatic factors, and changes in the landscape might influence the diet of Barn Owls (*Tyto alba*). Love et al. (2000), for example, found significant changes in diets of Barn Owls in the United Kingdom that they attributed primarily to changing agricultural practices. Taylor (1994) examined Barn Owl diets over 12 continuous years in a Scottish agricultural area and reported fluctuations in prey consumed related to cyclic changes in small mammal populations.

Barn Owls prey mainly on a wide variety of mammalian species over their cosmopolitan range (Taylor 1994, Bruce 1999, Marti et al. 2005); they eat mostly small, nocturnal mammals (Herrera and Jaksic 1980, Jaksic et al. 1982), only occasionally capturing birds at high frequencies (Brosset 1956, Görner 1978). Barn Owl diets have been studied most intensively in the United States and Europe (Campbell et al. 1987, Taylor 1994, Marti et al. 2005), but also in South America (Jaksic et al. 1982, Bellocq 2000), Africa (Vernon 1972, Goodman 1986), Asia (Lenton 1984, Mahmood-Ul-Hassan et al. 2007), and Australia (Morton and Martin 1979, Palmer 2001). The broad geographic distribution and the large quantity of published dietary information make the Barn Owl a good candidate for understanding factors that affect diet variation.

Collectively, the large number of published studies provide an overview of the diet of Barn Owls, including types of prey taken (Taylor 1994, Bruce 1999, Marti et al. 2005), size of prey (Dickman et al. 1991, Ille 1991, Marti et al. 1993), habitats used (Begall 2005, Bond et al. 2004, Askew et al. 2007), effect of season on diet (Baudvin 1983, Campbell et al. 1987), and the influence of climate on diet (Avery 1999, Jaksic and Lazo 1999). However, most studies of Barn Owl diets have been short-term and at risk of being biased because data were often collected during a single season or year and, at times, during atypical conditions, e.g., abnormal weather or in areas with unusual prey populations (Heywood and Pavey 2002, Sahores and Trejo 2004, Altwegg et al. 2006). Short-term studies, thus, cannot provide insight into the dynamics of predation.

I studied Barn Owls in a north-temperate agricultural area with the objectives to: (1) describe the diet over a 15-year period, (2) quantify the effects of weather variation on the diet, and (3) quantify the impact of vegetation changes on the diet.

METHODS

Study Area.—I studied Barn Owls in an area of ~1,000 km^2 in Box Elder, Davis, and Weber counties, Utah. The area was in a long, narrow, and essentially flat valley at an elevation of 1,300 m between the Wasatch Mountains and the Great Salt Lake (41° 01′ N, 112° 11′ W). The area was formerly shrub-steppe desert, but the natural plant community has been supplanted by irrigated agriculture and urban development. Primary crops were hay, corn, wheat, barley, and some livestock pasture. Uncultivated land was limited to narrow strips along roads, water courses, borders of agricultural fields, and adjacent to the Great Salt Lake. Annual precipitation averaged 35 cm, and mean temperatures for January and July were −3.5° C and 23.9° C,

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respectively (http://www.ncdc.noaa.gov/oa/ncdc.html). Barn Owls, resident on the study area, occasionally nested in old buildings and haystacks, but most used nest boxes (Marti 1997).

Source of Data.—Collection sites were nest boxes placed individually in abandoned agricultural silos (Marti et al. 1979); I visited all boxes and collected regurgitated pellets each month from 1977 to 1991. Boxes were placed throughout the study area with locations dictated by availability of silos. I identified and quantified prey items in pellets using standard methods (Marti et al. 2007). The smallest sampling unit for diet analyses consisted of prey from 1 month at one collection site. These samples were combined for analyzing diets by season or year.

Description of Food-niche Breadth.—Food-niche breadth (FNB) is a measure of dietary diversity incorporating measures of the number of kinds of prey eaten and the relative proportions of the kinds of prey in the diet. I prepared dietary data for describing FNB by identifying mammalian prey to species. Birds were also identified to species when possible, but insects were identified only to class. I estimated food-niche breadth (FNB) using the formula:

$$\mathrm{FNB} = 1 \Big/ \sum p_i^2,$$

where p_i is the proportion of prey category $_i$ (each kind of prey identified) in the Barn Owl diet (Levins 1968). Larger values of this index indicate a higher dietary diversity.

Environmental Variables.—I obtained climatic data—air temperature, precipitation, and number of days with snow on the ground—from National Climatic Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html) weather stations in the study area and calculated daily means for data recorded at three stations for use as variables that might explain changes in FNB. Variation in ambient temperature can influence prey use because changes in temperature may alter prey activity and affect the quantity of food needed by Barn Owls. Precipitation may directly influence Barn Owl hunting activity and indirectly affect prey population size and availability through its influence on vegetation. Snow cover may also affect prey use because some prey species, particularly voles (*Microtus* spp.), burrow under the snow, making them less vulnerable to owl predation.

Vegetation composition may also affect Barn Owl diets. My study area was agricultural land with interspersed housing developments and most vegetation was not native. I obtained annual crop data—number of hectares of each major crop planted—from the U.S. Department of Agriculture (http://www.nass.usda.gov) for use as explanatory variables of FNB. I calculated an annual crop-diversity index using the same formula used for calculating FNB and then compared it among seasons and years using PROC GLM (SAS Institute 2000).

Dietary Variation.—I used contingency table analysis (PROC REGR) (SAS Institute 2000) to evaluate changes in prey frequencies. Variation in diet was further evaluated by comparing FNB among years and seasons (spring [Mar–May], summer [Jun–Aug], fall [Sep–Nov] and winter [Dec–Feb]) and years using PROC GLM (SAS Institute 2000).

Variation in Food-niche Breadth.—I used multiple linear regression (PROC GLM) (SAS Institute 2000) to examine the relationship of FNB with candidate explanatory variables. The available variables were: mean annual precipitation; mean annual daily temperature; number of days with deep snow cover; hectares planted to hay, wheat, corn, and barley; and the annual diversity of crops planted. I did not include mean daily temperature or crop diversity in model selection because those variables did not vary significantly among years. The fit between candidate models and the data was evaluated using Akaike's information criterion (Burnham and Anderson 2002). I reported the adjusted R^2 to assist in evaluating the overall fit of the candidate models.

RESULTS

Food-niche Description.—I identified 111,016 prey items from 1,426 monthly samples collected at 31 sites. Owls consumed at least 26 species of prey, but 93.6% of the prey items were voles (75.9%; *Microtus pennsylvanicus* and *M. montanus*) and mice (17.7%; *Peromyscus maniculatus*, *Reithrodontomys megalotis*, and *Mus musculus*; Table 1). The number of prey items collected each year (1977 = 10,043; 1978 = 7,784; 1979 = 13,607; 1980 = 9,069; 1981 = 9,460; 1982 = 7,437; 1983 = 9,306; 1984 = 6,181; 1985 = 2,413; 1986 = 4,247; 1987 = 9,370; 1988 = 6,809; 1989 = 4,055; 1990 = 6,688; 1991 = 4,547) varied among years in relation to the number of nesting Barn Owls ($r_s = 0.59$, $P < 0.02$).

FNB was 3.33 when calculated with all prey items combined ($n = 111{,}016$), whereas the mean

TABLE 1. Diet of a Barn Owl population in northern Utah, 1977–1991.

	Number in diet (%)	% Occurrence at 31 collection sites	% Occurrence in 1,426 pellet collections
Mammals	109,035 (98.2)	100.0	100.0
Sorex vagrans	4,223 (3.8)	100.0	70.1
Myotis spp.	8 (tr.[a])	16.1	0.4
Eptesicus fuscus	7 (tr.)	6.5	0.1
Sylvilagus nuttalii (neonate)	3 (tr.)	9.7	0.2
Thomomys talpoides	649 (0.6)	54.8	8.6
Perognathus parvus	2 (tr.)	6.5	0.1
Reithrodontomys megalotis	6,157 (5.9)	100.0	74.7
Peromyscus maniculatus	6,853 (6.2)	100.0	82.6
Ondatra zibethicus (juvenile)	40 (tr.)	35.5	1.7
Microtus pennsylvanicus	42,718 (38.5)	100.0	99.2
M. montanus	41,527 (37.4)	100.0	99.3
Rattus norvegicus (juvenile)	308 (0.3)	90.3	13.2
Mus musculus	6,193 (5.6)	100.0	78.2
Mustela frenata	1 (tr.)	3.2	0.1
Birds	2.5 (1.8)	96.4	50.6
Rallus limicola	4 (tr.)	12.9	0.3
Porzana carolina	76 (tr.)	51.6	2.9
Charadrius vociferus	1 (tr.)	3.2	0.1
Recurvirostra americana	1 (tr.)	3.2	0.1
Gallinago gallinago	16 (tr.)	16.1	0.6
Columba livia	23 (tr.)	35.5	1.4
Tyto alba (nestling)	1 (tr.)	3.2	0.1
Cistothorus palustris	36 (tr.)	29.0	1.3
Sturnus vulgaris	382 (0.3)	90.3	15.3
Sturnella neglecta	11 (tr.)	19.4	0.6
Passer domesticus	146 (0.1)	74.2	5.0
Unidentified blackbird[b]	198 (0.2)	90.3	8.8
Unidentified small bird (~20 g)	603 (0.5)	93.5	22.3
Unidentified small bird (~40 g)	455 (0.4)	100.0	17.7
Insects, unidentified	14 (tr.)	29.0	0.8

[a] tr. = <0.1%.
[b] Red-winged (*Agelaius phoeniceus*) or Yellow-headed (*Xanthocephalus xanthocephalus*) blackbirds.

FNB of the 1,426 monthly samples was 2.78 (SD = 0.85, range = 1.07–8.7). FNB varied among years ($F_{14,399} = 4.1$, $P = 0.0001$), gradually decreasing during the study (Fig. 1). FNB differed significantly between consecutive years only for 1979 and 1980 ($F_{1,57} = 6.96$, $P = 0.01$) and 1987 and 1988 ($F_{1,58} = 12.0$, $P = 0.001$). The decrease

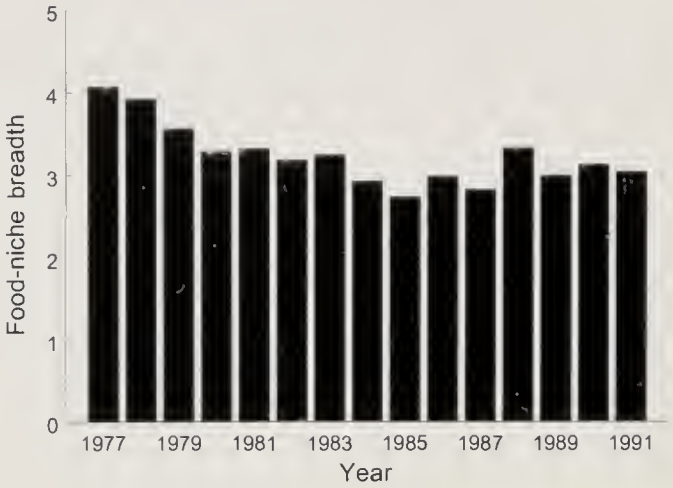

FIG. 1. Barn Owl food-niche breadth in northern Utah by year.

in FNB was correlated with an increase in the frequency of voles in the diet ($r_s = -0.99$, $P < 0.0001$). Overall, FNB varied among seasons (Fig. 2) and, although FNB was not statistically different among seasons ($F_{3,56} = 2.4$, $P = 0.07$), the pattern observed may be biologically significant.

Environmental Variability.—Total precipitation varied among years ($F_{14,28} = 11.8$, $P = 0.0001$), but mean daily temperature did not ($F_{14,165} = 0.2$, $P = 0.99$). The number of days with snow sufficiently deep (>15 cm) to interfere with prey detection and capture by Barn Owls also varied among years ($F_{14,75} = 3.4$, $P = 0.0003$). The frequency of voles in the diet of Barn Owls during winters having the greatest number of days with deep snow was less than in milder winters, but the relationship was not significant ($F_{1,14} = 0.16$, $r^2 = 0.01$, $P = 0.69$). Winters when the ground was covered longest with deep snow were followed by

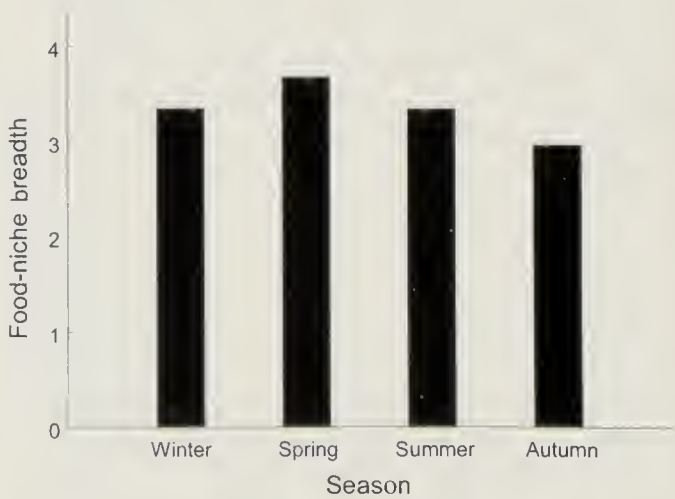

FIG. 2. Barn Owl food-niche breadth in northern Utah by season, years 1977–1991 combined.

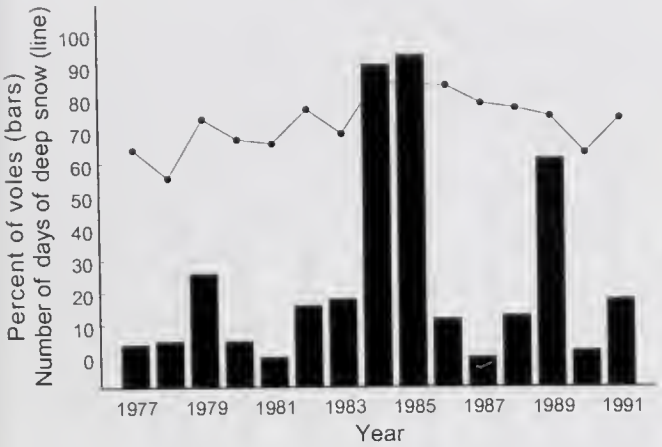

FIG. 3. Number of days with deep snow (>15 cm) on ground (bars) in northern Utah and frequency of voles in the diet (line) of Barn Owls during spring.

a significant increase in the frequency of voles in spring Barn Owl diets ($F_{1,14} = 7.79$, $r^2 = 0.32$, $P = 0.01$; Fig. 3). Summer diets following winters with deep snow cover also contained a higher frequency of voles ($F_{1,14} = 4.6$, $r^2 = 0.26$, $P = 0.05$). The same relationship continued into autumn but the trend was not significant ($F_{1,14} = 1.5$, $r^2 = 0.1$, $P = 0.25$).

The number of hectares planted in different crops varied among years with the number of hectares of hay increasing during the study and the area devoted to other crops decreasing (Fig. 4). Crop diversity did not vary among years ($F_{11,35} = 1.0$, $r^2 = 0.32$, $P = 0.45$).

Dietary Variation.—Frequencies of different prey items consumed did not vary among years ($\chi^2 = 64.3$, df = 70, $P = 0.67$; Fig. 5), among seasons for all years combined ($\chi^2 = 6.4$, df = 15, $P = 0.97$), or among seasons within years. The percentage of voles (both species combined) in the diet of Barn Owls varied by an average of only 2.9% from year to year ($\chi^2 = 4.6$, df = 14, $P = 0.99$).

Variation in Food-niche Breadth.—The model that best explained variation in FNB among years included the variables: hectares of hay planted, hectares of corn planted, and hectares of barley planted (Table 2).

DISCUSSION

Barn Owls exhibited little variation in diet over a 15-year period in northern Utah where habitat changes were minimal and variation in precipitation was buffered by crop irrigation, minimizing the effects of year-to-year variation of precipitation on vegetation. In contrast to my findings, Taylor (1994) found pronounced fluctuation in Barn Owl diets corresponding to vole population cycles during a long-term study in Scotland. The proportion of voles in the diet of Barn Owls in my study, unlike several studies in Europe (Bohnsack 1966, de Bruijn 1979, Taylor 1994), did not show cyclic fluctuations, possibly because irrigated agriculture produced a consistent, high-quality

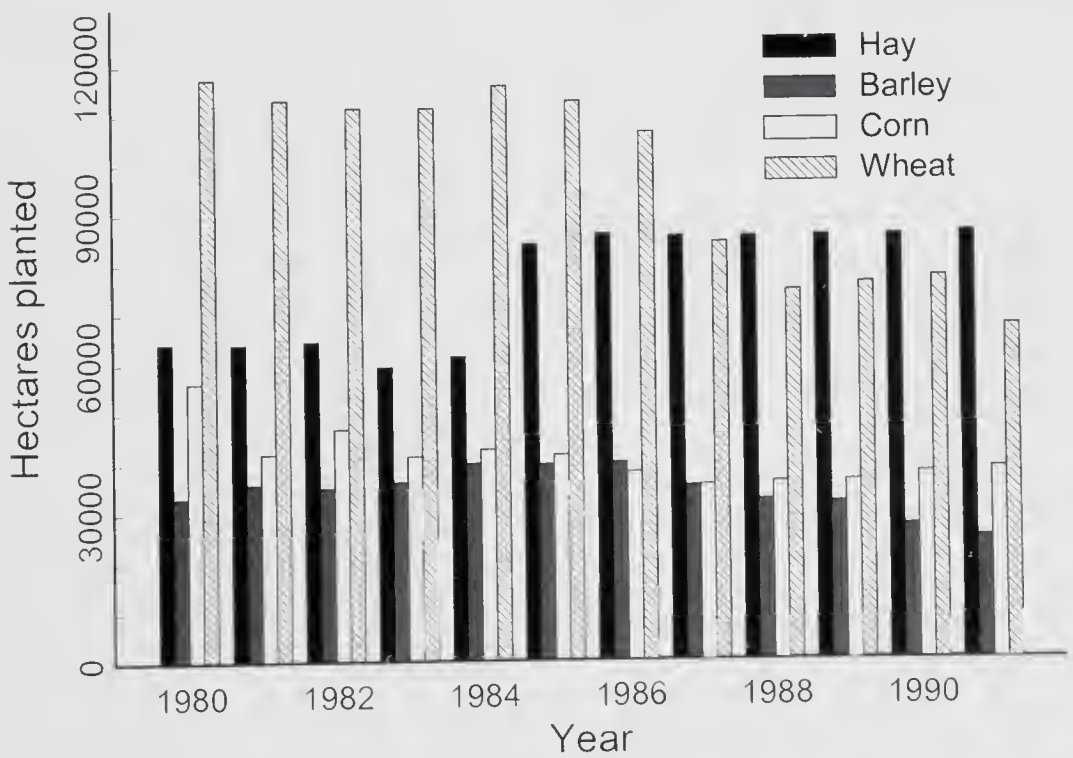

FIG. 4. Area (ha) planted in crops in northern Utah (data for hay were not available for 1977–1979).

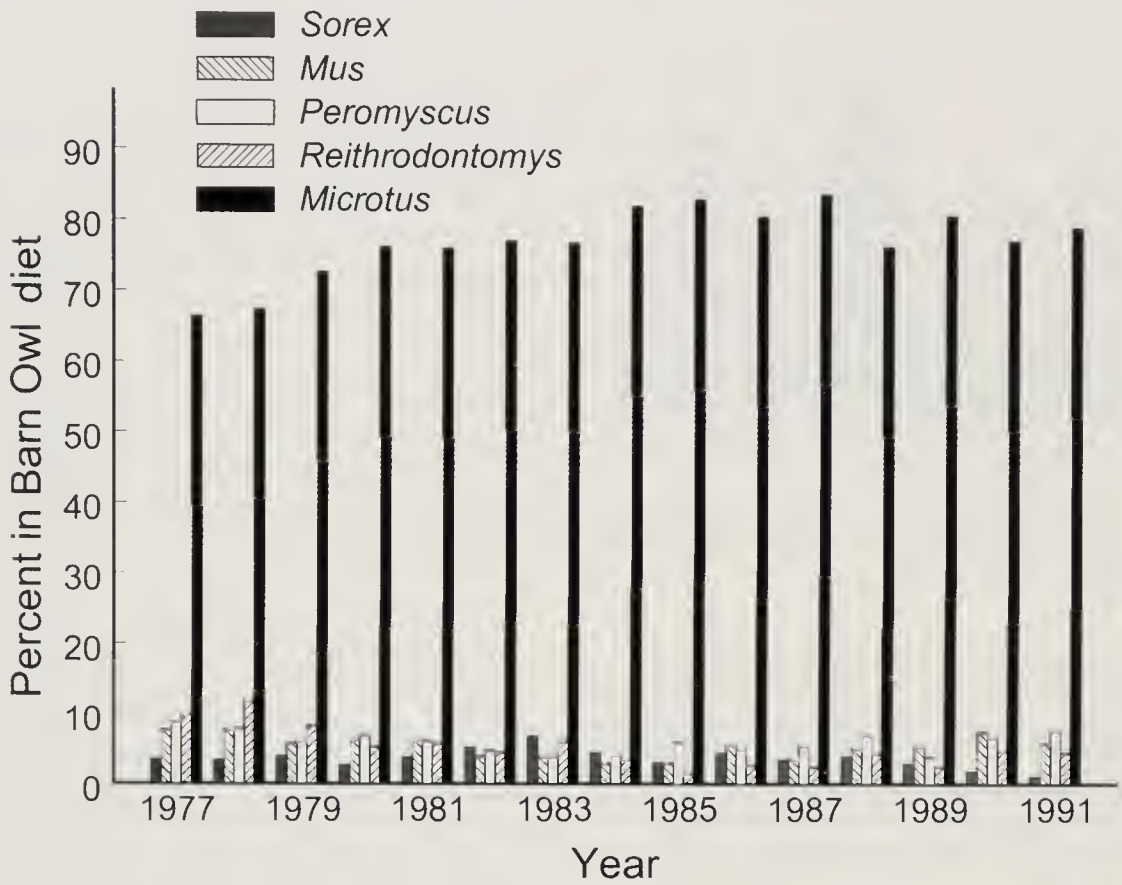

FIG. 5. Frequency of major prey in Barn Owl diets in northern Utah by year.

habitat that damped vole population fluctuations (Negus et al. 1986). Changes in Barn Owl diets sampled in two periods separated by a 19-year interval (1956–1974 and 1993–1997) in the United Kingdom were mostly attributable to a change from mixed-crop farms to more homogenous farms (Love et al. 2000). The mode of farming did not change during my study, but changes in proportion of crops planted did and those changes were related to the small changes in the diet—the more hay planted, the more voles in the diet. Voles are known to be abundant in forage crops like hay (Getz 1985), and Barn Owls in Utah may have concentrated their foraging in the vegetation that served as best vole habitat as they did in the United Kingdom (Askew et al. 2007).

Voles were the most common prey in the diet of Barn Owls in my study, and have been the most numerous prey of these owls in many other studies conducted in the north-temperate zone (Campbell et al. 1987, Taylor 1994, Bruce 1999). In studies where an index of small mammal population size was available, Barn Owls captured voles in greater proportion than expected based on relative abundance (Marti 1974, Colvin 1984, Askew et al. 2007). The high proportion of voles in the diet of Barn Owls in my study also suggests that voles were taken selectively. I found strong evidence of selective predation by Barn Owls on voles inhabiting an island in the Great Salt Lake 10 km from the present study area, probably due to the owls hunting preferentially in vole habitat (Marti 1986); Barn Owl diets on that island contained 81% voles by number despite vole habitat being extremely limited. Voles were not known to occur on Antelope Island prior to my finding them in the Barn Owl diet (Bowers 1982,

TABLE 2. Models of variation in food-niche breadth among years using seven explanatory variables: annual precipitation (AP), number of days with deep snow on ground (DDS), hectares of corn planted (HC), hectares of hay planted (HH), hectares of barley planted (HB), and hectares of wheat planted (HW).[a]

Model	Δ_i[b]	w_i[c]	Adj. R^2
HH + HC + HB	0	0.962	0.99
HC + DDS + AP	6.65	0.035	0.99
HH + HC + HW	12.78	0.002	0.96
HH + HB + AP	14.11	0.001	0.95
HH + HC + AP	14.91	0.001	0.94

[a] Akaike's information criterion (AIC) for the best model was −42.83.
[b] Δ_i = difference between the AIC value of a given model and that of the best-fitting model.
[c] w_i = AIC model weight.

Marti 1986). A similar pattern was seen in southwestern Idaho where frequency of voles was higher in Barn Owl diets at nests surrounded by irrigated agricultural land (Marti 1988). Barn Owls appeared to concentrate their foraging in habitats where voles were most numerous both on Antelope Island and in southwestern Idaho.

Fast and Ambrose (1976) and Derting and Cranford (1989) found that captive Barn Owls selected *Microtus* over *Peromyscus* when given a simultaneous choice. Prey size may be an important factor in prey selection—*Microtus* are about twice the mass of *Peromyscus* and *Mus*, the next largest among the most commonly taken prey in my study. Captive Barn Owls, given a simultaneous choice between two sizes of the same species, selected larger prey up to the point where prey became hard to subdue (Ille 1991).

It seems likely that Barn Owls may not discriminate between the two vole species because both are found in the same habitats (Getz 1985), and are similar in appearance and mass. A sample of voles trapped near my study area (University of Utah Museum collection; H. J. Egoscue, unpubl. data) revealed no difference in mass between the species ($t = 1.53$, df = 63, $P = 0.13$). Despite these similarities, I separated the two voles in my analyses because I did not know whether Barn Owls can or do distinguish between them.

Tores et al. (2005) concluded that Barn Owls prefer the kind of prey that voles exemplify, but readily switch to different prey if the preferred species declines below a certain level. Barn Owls in Utah ate all of the small mammal species known to occur in the area (Newey 1951, Frost 1970). Some prey were available or vulnerable only at certain times of the year; seasonal variation in uncommon prey was most noticeable for northern pocket gophers (*Thomomys talpoides*), which were numerous in the diet in May when young animals disperse above ground (Nowak 1991). Birds were a minor component of the diet, and the frequency of some species in the Barn Owl diet could be attributed to migration. Sora (*Porzana carolina*), for example, occurred in the diet only in spring and early summer. Others, like European Starlings (*Sturnus vulgaris*), were not migratory and Barn Owls preyed on them throughout the year. However, starlings reached their highest numbers in the Barn Owl diet in winter when communal roosting may have made them more vulnerable.

I observed the same pattern of seasonal variation in the diet of Barn Owls in Utah that Taylor (1994) reported in Scotland—frequency of voles in the diet was lowest in spring, increased into summer, and peaked in late fall and early winter. During winters with more days of deep snow cover, Barn Owls in my study preyed on fewer voles. Winter fluctuations were likely explained by voles under deep snow cover having reduced vulnerability to predators (Canova 1989, Halonen et al. 2007).

The number of Barn Owls breeding in the study area varied 12-fold over the study period (Marti 1994, 1997), primarily due to differences in severity of winter weather (Marti and Wagner 1985). However, owl population density did not influence the rate of predation on voles; owl density as indexed by the number of nest attempts per year was not correlated with the frequency of voles in the diet ($r_s = -0.25$, $P = 0.37$).

Diets of Barn Owls inhabiting this agricultural ecosystem exhibited remarkable uniformity over the long term. The measures I applied—FNB variation and prey frequencies—showed the diet of Barn Owls in my study exhibited little variation. The owls preyed primarily on voles at all collection sites and during all seasons and years, and the small changes that I found from year to year likely were the result of an increase in the amount of hay grown and a concomitant increase in vole numbers. The reverse—changing from grass-oriented agriculture to corn and soybeans—has been associated with declines of Barn Owl populations in Ohio (Colvin 1985). Variation in annual precipitation in my study area was mitigated by crop irrigation providing consistent moisture levels each year, and, in turn, consistent prey habitat. The only weather variable strongly associated with diet variation of Barn Owls in Utah was the number of days the ground was covered with deep snow which interfered with owls ability to prey on voles.

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REGIONAL VARIATION IN DIETS OF BREEDING RED-SHOULDERED HAWKS

BRAD N. STROBEL[1,3] AND CLINT W. BOAL[2]

ABSTRACT.—We collected data on breeding season diet composition of Red-shouldered Hawks (*Buteo lineatus*) in south Texas and compared these data, and those reported from studies elsewhere to examine large scale spatial variation in prey use in eastern North America. Red-shouldered Hawk diets aligned into two significantly different groups, which appear to correlate with latitude. The diets of Red-shouldered Hawks in group 1, which are of more northern latitudes, had significantly more mammalian prey and significantly less amphibian prey than those in group 2, which are at more southerly latitudes. Our meta-analysis demonstrated the dietary flexibility of Red-shouldered Hawks, which likely accounts for their broad distribution by exploiting regional variations in taxon-specific prey availability. *Received 27 April 2009. Accepted 28 August 2009.*

Red-shouldered Hawks (*Buteo lineatus*; hereafter RSHA) were once considered the most abundant raptor in moist woodlands of North America (Bent 1937), and are thought to prefer mature contiguous forests, especially those associated with wetlands (Craighead and Craighead 1956, Bednarz and Dinsmore 1981, Dykstra et al. 2008). Breeding Bird Survey data indicate RSHA populations have declined in portions of the midwestern and northeastern United States, while populations in other areas appear to be relatively stable or increasing (Sauer et al. 2008). Population declines have heightened concern and protection for RSHA by several state agencies (Jacobs and Jacobs 2002).

Conversion of forests to agriculture is one factor thought to have contributed to RSHA population declines (Bednarz and Dinsmore 1981, Gehring 2003, Dykstra et al. 2008). Greater amounts of forest edge and smaller forest stand size caused by agricultural and silvicultural practices may provide a competitive advantage for habitat generalist raptors such as Red-tailed Hawks (*Buteo jamaecensis*) (Bednarz and Dinsmore 1981). Wetland degradation and drainage may also have reduced the quality and availability of foraging areas important to RSHAs (Jacobs and Jacobs 2002). Other studies have documented apparently sustainable RSHA populations in highly human altered landscapes (e.g., Bloom et al. 1993, Rottenborn 2000, Dykstra et al. 2001), suggesting that factors other than habitat alteration may be directly or indirectly contributing to RSHA population trends. For example, Bloom (1989) suggested that habitat use by RSHAs is strongly influenced by prey availability. The abundance and diversity of prey available to breeding RSHAs is likely associated with, and influenced by, landscape characteristics within RSHA foraging habitat.

Previous studies of breeding season diets indicate RSHAs use a variety of prey items across their range. Diets documented for RSHAs nesting in Missouri were primarily amphibians and reptiles (Parker 1986), while nearly 75% of the diets of RSHAs nesting in Maryland were mammals (Portnoy and Dodge 1979). The diets of breeding RSHAs in Arkansas (Townsend 2006) and Texas (Strobel 2007), in contrast, were largely invertebrates. Bednarz and Dinsmore (1985) documented RSHA dietary differences between two breeding seasons in Iowa, apparently associated with annual differences in precipitation and riparian flooding. Thus, it appears RSHAs adapt to some natural and anthropogenic landscape changes, likely facilitated by their ability to exploit a diverse suite of prey.

Regional variation in prey use by RSHAs is likely caused by large-scale ecological differences such as precipitation patterns, temperature variation, and composition of vegetation communities influencing prey communities. Anthropogenic changes to the landscape have also influenced population trends of RSHAs in North America (Brown 1971, Henny et al. 1973, Peterson and Crocoll 1992, Jacobs and Jacobs 2002). Understanding the coarse scale patterns in prey use, and the breadth and plasticity of RSHA diets may

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offer insights into productivity and ecology of RSHA populations that would facilitate development of sound conservation strategies for the species. We used breeding season food habits information from our study in south Texas and published studies conducted on breeding RSHA populations east of the Continental Divide to examine large scale spatial variation in prey use by eastern populations of Red-shouldered Hawks in North America.

METHODS

Study Area and Field Procedures.—We located active Red-shouldered Hawk nests on the Rob and Bessie Welder Wildlife Refuge and Twin Oaks Hunting Resort in San Patricio and Refugio counties (respectively), Texas. Nests of breeding RSHA pairs were located using broadcast survey methods as described by McLeod and Andersen (1998) and intensive systematic nest searching between April and July 2005 and 2006. We installed color video surveillance cameras (Models OC-225 and C3320AX, Clover Electronics®, Cerritos, CA, USA) after eggs hatched and young were ~1 week of age. We recorded all diurnal activities using time-lapse VCRs (Piczel video security products® and Security Labs®, Noblesville, IN, USA) until each nesting attempt was completed. We based our analysis on prey items delivered to nestlings prior to fledging to reduce bias caused by off camera prey deliveries. We identified prey items to the most specific taxa possible using regional field guides, museum specimens, and Welder Wildlife Refuge staff expertise (Strobel 2007).

Literature Search.—We conducted a literature search for published studies (peer reviewed publications, books, and theses) of RSHA breeding season diet. Methods used in other studies included: direct visual observation, video surveillance, identification of uneaten prey remains, composition of regurgitated pellets, and crop contents analysis. We classified methods of the publications as either direct observation (DO) or prey remains analysis (PR).

Inconsistent methods of data collection are a common concern in meta-analysis and the potential biases of different techniques to assess diets of raptors have been noted previously (Redpath et al. 2001, Rogers et al. 2005, Marti et al. 2007). Results from studies using prey remains analysis can be skewed by higher persistence rates of heavy boned prey species, such as mammals, and falsely indicate higher frequency of occurrence of those species (Marti et al. 2007). Correct identification of prey items in direct observation studies often depends on prey item size and its distance from the observer (Marti et al. 2007). We attempted to reduce these potential confounding effects by pooling prey types into five taxonomic categories: mammals, birds, reptiles, amphibians, and invertebrates. When studies used multiple methods (i.e., DO and PR) to collect data and presented those data separately, we only used those collected through direct observation and excluded unknown or unidentified prey items (Table 1). Some studies presented yearly data separately and, to remain consistent in our analyses, we pooled all data from multiple years within those studies.

Statistical Analyses.—We calculated the Pearson's correlation coefficient, based on the proportion of prey types reported in each study to compare RSHA diets among studies (Krebs 1999). Values of Pearson's correlation coefficient range from 0 to 1 indicating no dietary overlap (0) to complete dietary overlap (1). We used the Pearson's correlation coefficient as the distance function within an unweighted pair-group method using arithmetic means (UPGMA) cluster analysis to calculate and compare the similarity of diets reported for breeding RSHAs. We assessed the significance of clusters using the approximately unbiased significance level ($P \approx 1\text{-}au$) calculated from 10,000 multiscale bootstrap iterations of the distance matrix using the PVCLUST package (Suzuki and Shimodaira 2006). We used Hotelling's T^2 test, in the ICSNP package, on the arcsine transformed proportions of each prey category to identify which prey categories contributed to the formation of significant clusters. Reported values represent means ± SD. Analyses were conducted using program R version 2.8.0 (R Development Core Team 2008).

RESULTS

We monitored prey use at 10 different Red-shouldered Hawk nests in south Texas in 2005 and 2006, and collected 1,457 hrs of video footage yielding 1,315 prey items categorized into the five taxonomic categories (Table 1). We located 11 other studies that reported the diets of breeding RSHAs in different states in the eastern United States (Table 1). Few multi-year studies identified prey delivered to individual nests or by individual RSHAs. Thus, the independence of

TABLE 1. Composition of diets of breeding Red-shouldered Hawks as reported in 12 studies across the eastern United States. Methods of data collection included direct observation (DO) and pellet and/or prey remains examination (PR). Shading indicates significantly similar groups identified though cluster analyses. Adapted from Dykstra et al. (2008).

State	Year	# of nests	# Prey items	Mammal		Bird		Reptile		Amphib.		Invert.		Method	Source
				#	%	#	%	#	%	#	%	#	%		
IA	1977–1978	7	115	41	36	3	3	3	3	38	33	30	26	DO	Bednarz and Dinsmore 1985
IN	1999–2000	8	195	82	42	17	9	48	25	8	4	40	21	PR	Gehring 2003
MA	1974	4	46	33	72	2	4	2	4	9	20	0	0	DO	Portnoy and Dodge 1979
MD	1978–1979	17	30	23	77	1	3	2	7	4	13	0	0	DO	Janik and Moser 1982
MI	1942/1948	29	1,428	583	41	228	16	311	22	68	5	238	17	PR	Craighead and Craighead 1956
NY	1939–1942	16	—	—	58	—	8	—	3	—	18	—	11	DO/PR	Ernst 1945[a,b]
OH	1997–2001	21	198	64	32	14	7	46	23	36	18	38	19	DO	Dykstra et al. 2003
WI	1973–1979	9	97	57	59	1	1	14	14	12	12	13	13	DO	Welch 1987
AR	2004–2005	20	1,139	69	6	4	0	171	15	523	46	372	33	DO	Townsend 2006
GA	1994	8	181	34	19	15	8	43	24	46	25	43	24	DO	Howell and Chapman 1998
MO	1982–1983	3	—	—	17	—	0	—	26	—	46	—	11	DO	Parker 1986[a]
TX	2005–2006	10	1315	197	15	63	5	412	31	107	8	536	41	DO	Strobel 2007

[a] Only reported the relative proportions of prey items to total diet.
[b] Invertebrates approximate because of small unknown proportion (<3%) of crayfish categorized as miscellaneous.

data within each study is unknown; however, we assumed that natural and stochastic processes (pair and territory fidelity, nest accessibility, etc.) were similar among study populations, which facilitated comparison among studies. These data, in combination with our data, describe the diets of three (*B. l. alleni*, *B. l. lineatus*, *B. l. texanus*) of the five currently recognized subspecies of RSHA.

The cluster analysis of the Pearson's correlation coefficient for the 12 study areas identified several significant clusters ($P < 0.05$) with a primary division creating two distinct groups (Fig. 1). Our results indicate significant divergences at several levels of correlation; however, we were most interested in the dichotomous nature of the results and focus further analyses on the two most distinct groups. We arbitrarily titled the groups. Group 1 was comprised of data from studies in Indiana, Iowa, Maryland, Massachusetts, Michigan, New York, Ohio, and Wisconsin. Group 2 was comprised of data collected in Arkansas, Georgia, Missouri, and Texas. Although grouped by similarity in breeding season diet, the latitude of each study site appears to correlate with group membership with studies in group 1 occurring in states of higher latitudes than studies in group 2.

Analyses of those data from the northern and southern groups indicated substantial differences existed between diets in the two primary clusters ($F_{5,7} = 8.1$, $P < 0.01$). Red-shouldered Hawk diets in group 1 had more mammalian prey than those in group 2 (group 1, $\bar{x} \pm SD = 53.2 \pm 20.3\%$, group 2 = $17.9 \pm 9.6\%$; $t_{11} = 3.8$, $P < 0.01$, Fig. 2). Diets of RSHAs in group 2 had a higher proportion of amphibians (group 1 = $11.2 \pm 6.2\%$, group 2 = $32.9 \pm 20.3\%$; $t_{11} = -2.7$, $P = 0.02$) than those in group 1 (Fig. 2). Avian, reptilian, and invertebrate prey items comprise similar proportions of RSHA diets in both groups. All studies using prey remains analysis were assigned to Group 1, suggesting the suspected biases previously discussed may have skewed their results; however, the latitudinal pattern still exists in direct observational studies (Table 1).

DISCUSSION

Our analysis indicated there are two groups of Red-shouldered Hawks distinguishable by their breeding season diet. Breeding pairs in group 1 preyed more frequently on mammals while those in group 2 preyed more frequently on amphibians. In addition to diet similarities, there also appears to be a coarse spatial relationship within groups. Most studies conducted at northern latitudes

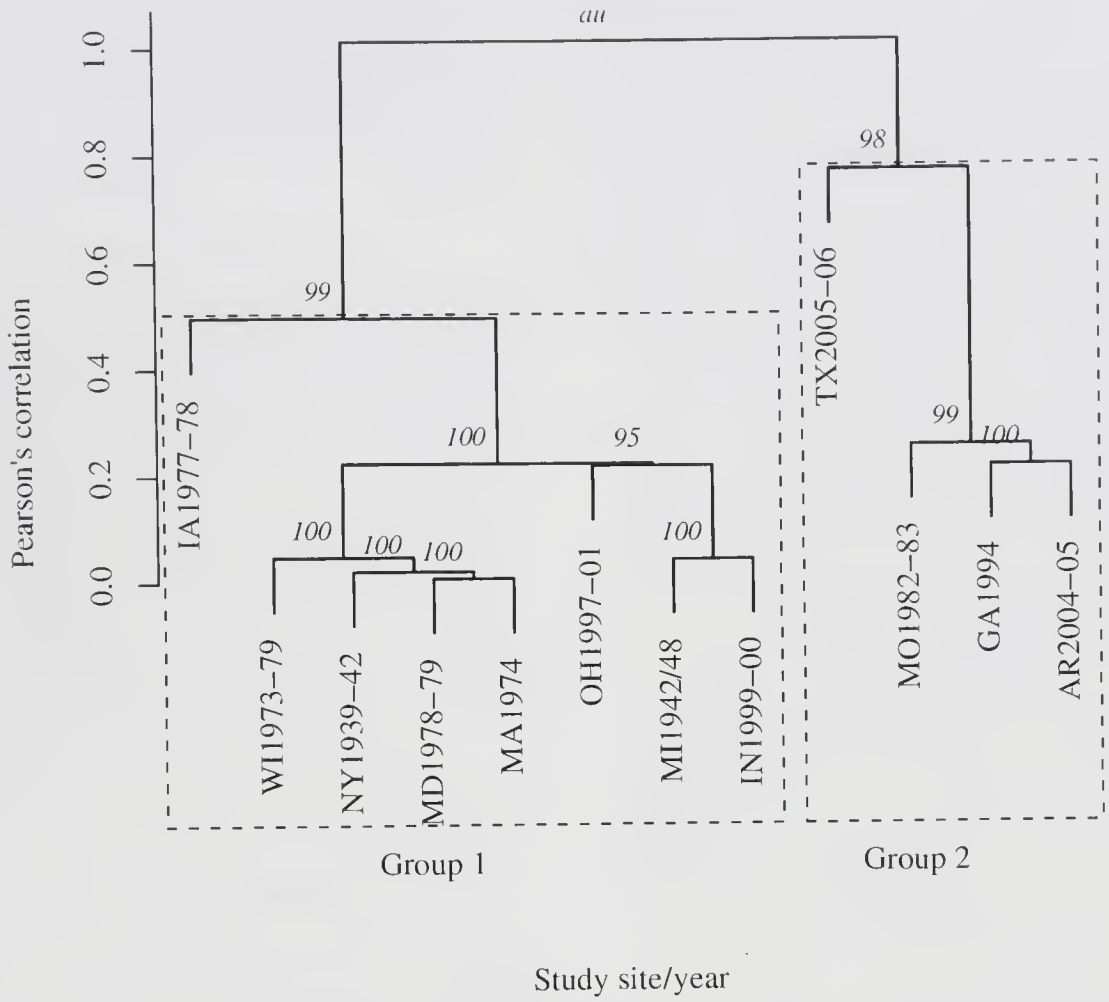

FIG. 1. Dendrogram illustrating similarity of diets of Red-shouldered Hawks reported by studies in 12 states across the eastern USA. *au* values indicate approximately unbiased significance level of each specified grouping ($P \approx 1$-*au*) based on 10,000 multiscale bootstrap iterations of the Pearson's correlation coefficient topology matrix of an UPGMA cluster analysis. Dashed boxes identify the primary significant ($P \leq 0.01$) groups.

(>38° N) were classified into group 1 and most southern latitude studies into group 2. We speculate the pattern between latitude and diet composition is ultimately caused by climate, vegetation, and precipitation patterns influencing prey type availability differently across North America. Results from Bednarz and Dinsmore's (1985) study in Iowa and Strobel's (2007) in Texas, support this hypothesis and show diets of RSHAs were primarily mammalian prey during drier conditions, but were primarily amphibian and invertebrate prey under conditions with abundant moisture. This may also explain why Bednarz and Dinsmore's (1985) and Strobel's (2007) data were the furthest diverged from other studies in their respective groups (Fig. 1).

The effects of latitude, temperature, and moisture regimes on species' distributions are largely accepted (MacArthur 1972), and clearly influence prey availability. These effects would presumably influence productivity and survival of RSHAs breeding in different areas of North America. For example, nutritional value varies widely among prey types and likely influences reproductive rates of RSHAs breeding in different regions of their range. Four studies in our analysis reported estimates of prey biomass and estimated mammalian prey items taken by RSHAs averaged 30% heavier than amphibian prey items (Howell and Chapman 1998, Dykstra et al. 2003, Townsend 2006, Strobel 2007). Strobel (2007) estimated that RSHAs breeding in south Texas deliver ~6,000 g of prey to a nest to fledge one nestling. Common Kestrels (*Falco tinnunculus*, Wiehn and Korpimäki 1997), European Starlings (*Sturnus vulgaris*, Wright et al. 1998), and RSHAs (Strobel 2007) increased prey delivery rates to meet the increased nutritional demands of larger broods or older nestlings. Red-shouldered Hawks breeding in areas with larger and more nutrient rich prey may be able to rear larger broods, fledge higher quality young, or allocate more time to activities

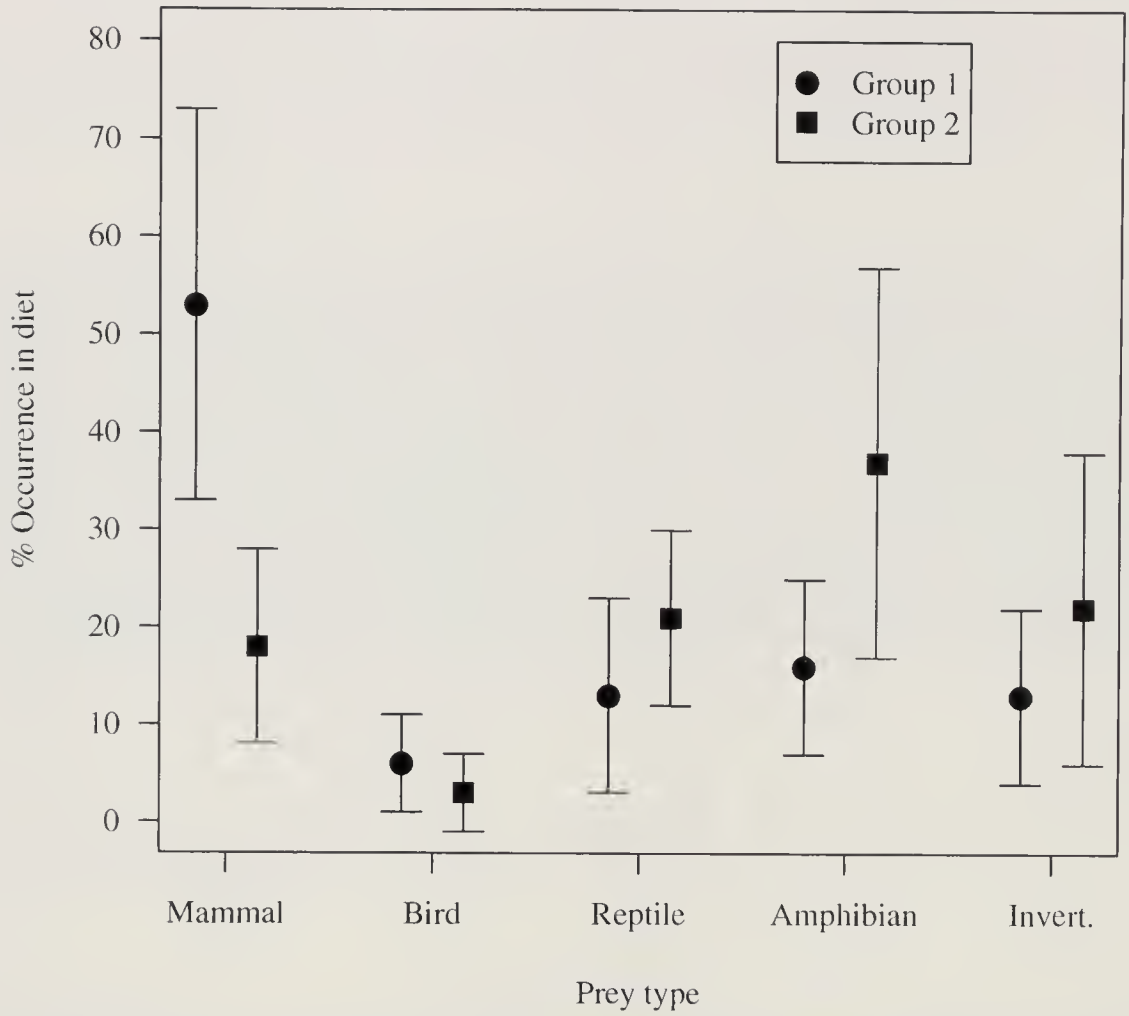

FIG. 2. Composition of Red-shouldered Hawk diets among studies in two significantly different groups (Group 1 = northern studies; Group 2 = southern studies) identified by 10,000 multiscale bootstrap iterations of the Pearson's correlation coefficient. Spreads indicate ±1 SD from the mean percent contributed by each of the five prey types.

such as nestling defense, and increase their productivity. A *post hoc* examination of productivity rates (average number of nestlings produced by successful nests) indicated little difference in productivity of RSHAs in group 1 or group 2 (2.42 ± 0.51, 2.38 ± 0.67; respectively). Bednarz and Dinsmore (1985) noted similar RSHA productivity on their study site between years when RSHAs had markedly different diets. This suggests RSHAs have similar productivity despite using different prey types. This also suggests different prey types result in differences in foraging effort, prey delivery rates, and energetic demands upon adults.

Recognizing patterns in prey use by RSHAs throughout North America may provide valuable insight for conservation planning. Breeding populations of RSHAs feeding primarily on mammalian prey items may not be as greatly influenced by wetland degradation as populations feeding primarily on amphibians, but may be more susceptible to fluctuations in forest harvest regimes or natural fluctuations in small mammal populations. It is unclear how factors like bioaccumulation of toxins and juvenile survival rates vary between populations with different breeding season diets. Few studies have examined regional specific survival patterns or lifetime reproductive success in widespread raptor populations, both of which are likely influenced by diet composition and prey availability. Evaluating the importance of different types of prey for RSHAs throughout North America would be greatly enhanced if future studies provided accurate estimates of local prey biomass and availability.

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of the Twin Oaks Hunting Resort. The use of trade, product, industry, or firm names or products is for informative purposes only and does not constitute an endorsement by the U.S. Government, U.S. Geological Survey, or Texas Tech University. This is Welder Wildlife Foundation Contribution Number 688.

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EFFECTS OF BROWN-HEADED COWBIRD PARASITISM ON PROVISIONING RATES OF SWAINSON'S WARBLERS

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ABSTRACT.—We studied the effects of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and other factors on food provisioning rates of Swainson's Warblers (*Limnothlypis swainsonii*), a secretive and poorly understood species of conservation concern. We used time-lapse video systems to collect provisioning data at 25 nests, nine of which were parasitized by Brown-headed Cowbirds. We found strong relationships between feeding rate and brood size with increases from 2.0 feeding visits/hr for nests with a single Swainson's Warbler nestling to 3.0/hr for broods of four. We also found an effect of nestling age with 1.9 visits/hr early and 3.2 visits/hr late in the nestling period. The relationships between cowbird parasitism and provisioning were complex. Nests with brood size of one or three that contained a single cowbird nestling had greater provisioning rates (2.5 and 3.3 visits/hr, respectively) than non-parasitized nests (2.0 and 2.6 visits/hr, respectively). Nests with two cowbirds and no Swainson's Warbler young had greater provisioning rates (3.4 visits/hr) than those with two warbler young (2.4 visits/hr), or one warbler and one cowbird (2.6 visits/hr). The increase in provisioning rate with nestling age was more pronounced with two cowbird nestlings present than in nests with zero or one cowbird nestling. These results suggest that parasitized nests, especially those with multiple cowbird nestlings, can impose greater energetic demands on parents. Food limitation may constrain the ability of Swainson's Warblers to adequately care for both their own nestlings and cowbird young. *Received 10 April 2009. Accepted 2 September 2009.*

Swainson's Warbler (*Limnothlypis swainsonii*) is a medium-sized wood warbler that occurs in dense understory vegetation in bottomland hardwood forests of the southeastern United States. Nondescript olive-brown coloration and secretive behavior make it elusive and difficult to locate and study. Swainson's Warblers have specialized breeding habitat requirements, preferring forest stands with dense understory vegetation, often of giant cane (*Arundinaria gigantea*) (Brewster 1885, Meanley 1971, Brown et al. 2009). Conversion of higher elevation bottomland hardwood forests and loss of canebrakes has reduced the availability of breeding habitat for Swainson's Warblers (Brown et al. 2009), likely contributing to the status of this species as among those of greatest conservation concern nationally (Hunter et al. 1993, Rich et al. 2004).

Fragmentation of bottomland hardwood forests has exposed some Swainson's Warbler populations to high frequency of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Benson et al. 2010a). Thirty-six percent of Swainson's Warbler nests in eastern Arkansas were parasitized (n = 135 nests), and 10% received multiple cowbird eggs (Benson et al. 2010a). Brood parasitism may be a major contributing factor for population declines of some songbirds (Schmidt and Whelan 1999). Cowbirds reduce the productivity of host species by removing or damaging eggs, and through competition between host and cowbird young (Trine et al. 1998, Hoover 2003). This competition may lead to starvation of host nestlings in parasitized nests, especially for smaller host species such as Swainson's Warblers (Benson et al. 2010a). Parasitism of smaller hosts may also reduce the growth rate of surviving nestlings (Dearborn et al. 1998, Burhans et al. 2000), leading to higher post-fledgling mortality. Parasitism of Swainson's Warblers in eastern Arkansas decreased productivity of successful nests from 2.75 in non-parasitized to 0.60 Swainson's Warbler young in parasitized nests (Benson et al. 2010a); parasitized nests with multiple Brown-headed Cowbird young produced no Swainson's Warbler young (Benson 2008).

Beyond the direct effects of parasitism, increased food provisioning resulting from parasitism also may have harmful effects on adults. Presence of cowbird young in nests of relatively small hosts may lead to increased prey delivery rates by the host parents (Hoover and Reetz 2006) and increase food demand from adults (Kilpatrick 2002). This increased parental investment may lower future reproductive investment (Gustafsson and Sutherland 1988, Lindén and Møller 1989). Increased activity at the nest may attract predators and lead to decreased survival of parasitized nests (Haskell 1994, Leech and Leonard 1997, Dear-

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born et al. 1998, Dearborn 1999, Tewksbury et al. 2002). The stress imposed on the host parents by increased provisioning rates may ultimately lead to lower survival or increased emigration rates of individuals with parasitized nests (Hoover and Reetz 2006).

We investigated food provisioning rates at parasitized and non-parasitized nests of Swainson's Warblers to understand why brood parasitism leads to decreased productivity and potential implications for conservation. We expected the food-delivery rate of adults to increase with parasitism due to the large size of young cowbirds relative to Swainson's Warblers. We also predicted multiple parasitism to have a greater impact than single parasitism, and for larger and older broods to receive more food deliveries than smaller and younger broods.

METHODS

Study Area.—We studied Swainson's Warbler breeding biology in 2006 and 2007 at White River National Wildlife Refuge (Brown et al. 2009). This >60,000-ha refuge is among the largest remaining areas of bottomland hardwood forest in the Mississippi Alluvial Valley (Twedt and Loesch 1999). Areas with Swainson's Warblers at White River National Wildlife Refuge were dominated by sugarberry (*Celtis laevigata*), sweetgum (*Liquidambar styraciflua*), box elder (*Acer negundo*), elm (*Ulmus* spp.), oak (*Quercus* spp.), sycamore (*Platanus occidentalis*), and hickory (*Carya* spp.). Dominant plants in the forest understory included greenbrier (*Smilax* spp.), Virginia creeper (*Parthenocissus quinquefolia*), peppervine (*Ampelopsis arborea*), grape (*Vitis* spp.), spicebush (*Lindera benzoin*), box elder, and dense thickets of giant cane.

Nest Searching and Video Monitoring.—We searched for Swainson's Warbler nests from late April to early August systematically by searching known territories with one to six observers, and opportunistically while engaged in other activities (Benson et al. 2010a). We recorded GPS (Global Positioning System) coordinates once nests were located, and returned at 1- to 4-day intervals to ascertain the status and fate of each nest (Benson et al. 2010a). We installed time-lapse video systems at a subset of nests as part of an effort to identify nest predators for this species (Benson et al. 2010b). These systems were a small color video camera (models PC506IR and PC168-IR, Supercircuits, Austin, TX, USA) mounted on 2.2-cm diameter wooden dowels; the camera was connected to a time-lapse VCR with two deep-cycle batteries >10 m from the nests in plastic weatherproof containers. Camera systems were camouflaged to blend in with surroundings; the presence of cameras appeared to not affect nest survival (Benson et al. 2010b). We returned to video-monitored nests at 1- to 4-day intervals to change batteries and tapes until nests failed or fledged young.

Video Processing.—We collected data on food provisioning rates of adult Swainson's Warblers at 25 nests, nine of which were parasitized by Brown-headed Cowbirds. We recorded the time of each feeding event for each nest.

Data Analyses.—We assessed the effect of Brown-headed Cowbird parasitism on Swainson's Warbler provisioning rates (feedings/hr) using repeated-measures ANOVA (SAS PROC MIXED) (Littell et al. 2006). We examined differences among nests containing no, one, and two cowbird nestlings to document the effect of parasitism. Other factors, including brood size and age of nestlings, may affect provisioning rates, and we tested for the influence of brood size, nest period (1–4, 5–8, and 9–12 days), and interactions among parasitism and these two factors. We set significance at $\alpha = 0.05$, and followed significant main effects or interactions with pair-wise contrasts. We considered nest, hour within nest, and day within nest as random effects to account for potential non-independence of observations, and used the Kenward-Roger approximation for denominator degrees of freedom (Littell et al. 2006). We incorporated brood size as a time-specific factor; consequently, nests were often observed with multiple brood sizes and fit into more than one category. We inspected the distribution of residuals and plots of residual versus predicted values to confirm our data conformed to the assumptions of normality and homogeneity of variances.

RESULTS

The mean brood size for the 16 non-parasitized nests was 2.86 (SE = 0.22; range = 1–4), and the mean brood size for parasitized nests (including cowbirds) was 2.67 (SE = 0.33; range = 1–4). The parasitized nests consisted of seven with one cowbird nestling and two with two cowbird nestlings.

We recorded 6,320 feeding visits ($\bar{x}$ = 252.8/nest, SE = 24.1, range = 28–465) between 17 May and 25 July 2006 and 2007, and data were

TABLE 1. Repeated-measures ANOVA examining the influence of number of Brown-headed Cowbird (BHCO) nestlings, brood size, nest period (1–4, 5–8, and 9–12 days = nestling age), and interactions among these factors on Swainson's Warbler provisioning rates at White River National Wildlife Refuge, Arkansas, 2006 and 2007.

Effect	df	*F*	*P*
BHCO	2, 34	4.08	0.026
Brood size	3, 307	9.89	<0.001
Nest period	2, 291	35.92	<0.001
BHCO × brood size	5, 276	2.53	0.029
BHCO × nest period	4, 235	5.36	<0.001
Brood size × nest period	6, 326	0.72	0.64
BHCO × brood size × nest period	5, 297	0.64	0.67

collected from 2 to 12 days for each nest ($\bar{x}$ = 8.4, SE = 0.6) representing 2,495 total nest hours ($\bar{x}$ = 99.8, SE = 7.7, range = 18–160). There was no significant three-way interaction among number of cowbird nestlings, brood size, and nest period, nor was there a significant interaction among brood size and nest period (Table 1). There were significant interactions between number of cowbird nestlings and brood size, and number of cowbird nestlings and nest period (Table 1).

Provisioning rate increased with brood size for non-parasitized nests ($t \geq 1.88$, $P \leq 0.06$; Fig. 1). The provisioning rate for nests with one cowbird nestling was similar to that for nests with a cowbird and a warbler nestling ($t = -0.49$, $P = 0.63$), but the rates for both nest types differed from nests with a single cowbird and two or three warbler nestlings ($t \geq 3.09$, $P \leq 0.002$). Nests with two cowbird nestlings and zero or one warbler nestling had similar provisioning rates ($t = 1.27$, $P = 0.21$). There was a marginally significant difference in provisioning rate between nests with a single warbler and a single cowbird nestling ($t = -1.83$, $P = 0.07$), and a significant difference between nests with three warbler

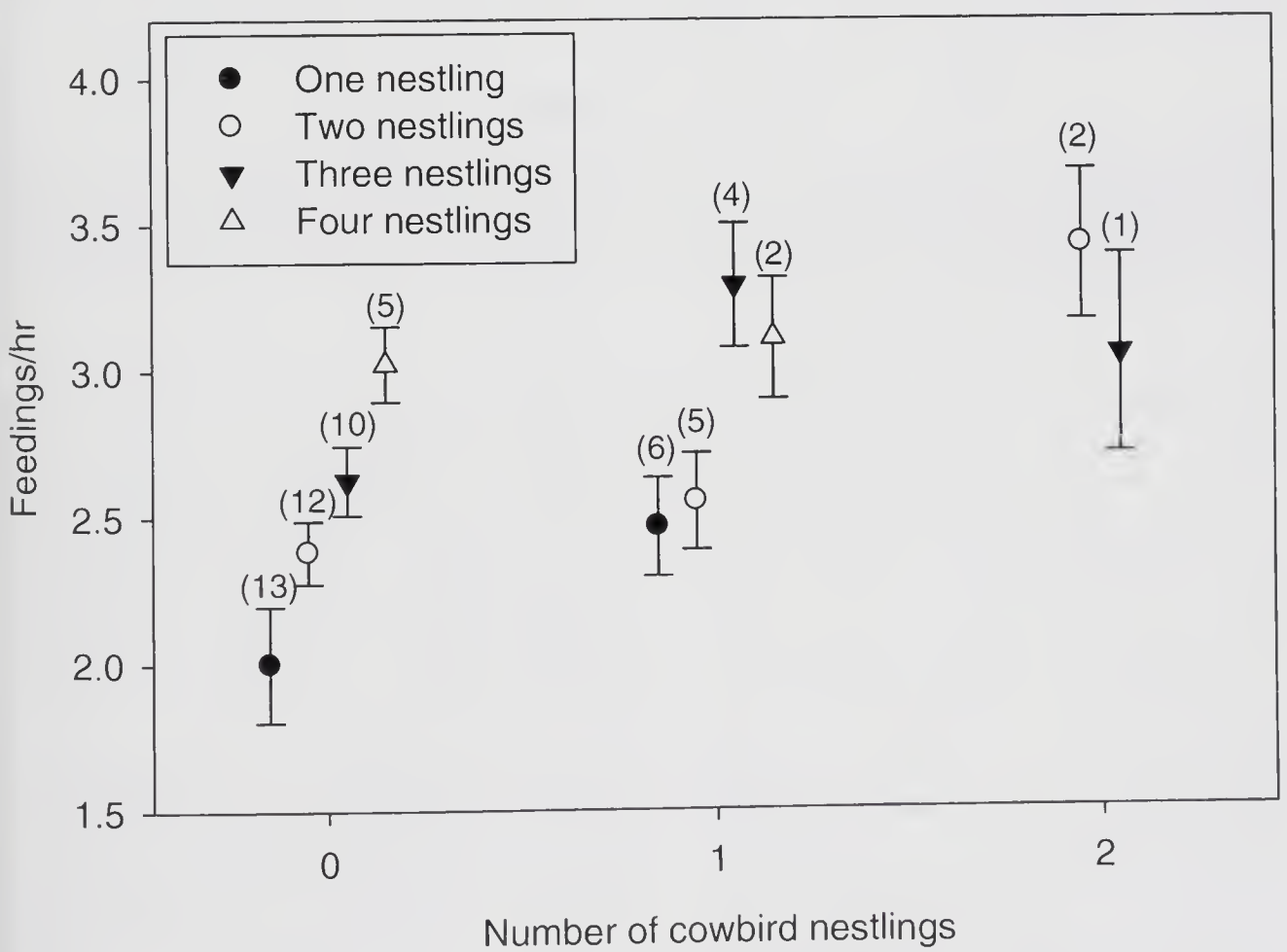

FIG. 1. Effects of Brown-headed Cowbird parasitism on provisioning rate (feedings/hr ± SE) at Swainson's Warbler nests for brood sizes of one through four (including cowbird young). Data were collected from 16 non-parasitized and nine parasitized nests at White River National Wildlife Refuge, Arkansas, 2006 and 2007. The sample size of nests for each category is in parentheses; most nests were observed at multiple states and do not equal sums of the total number of nests observed.

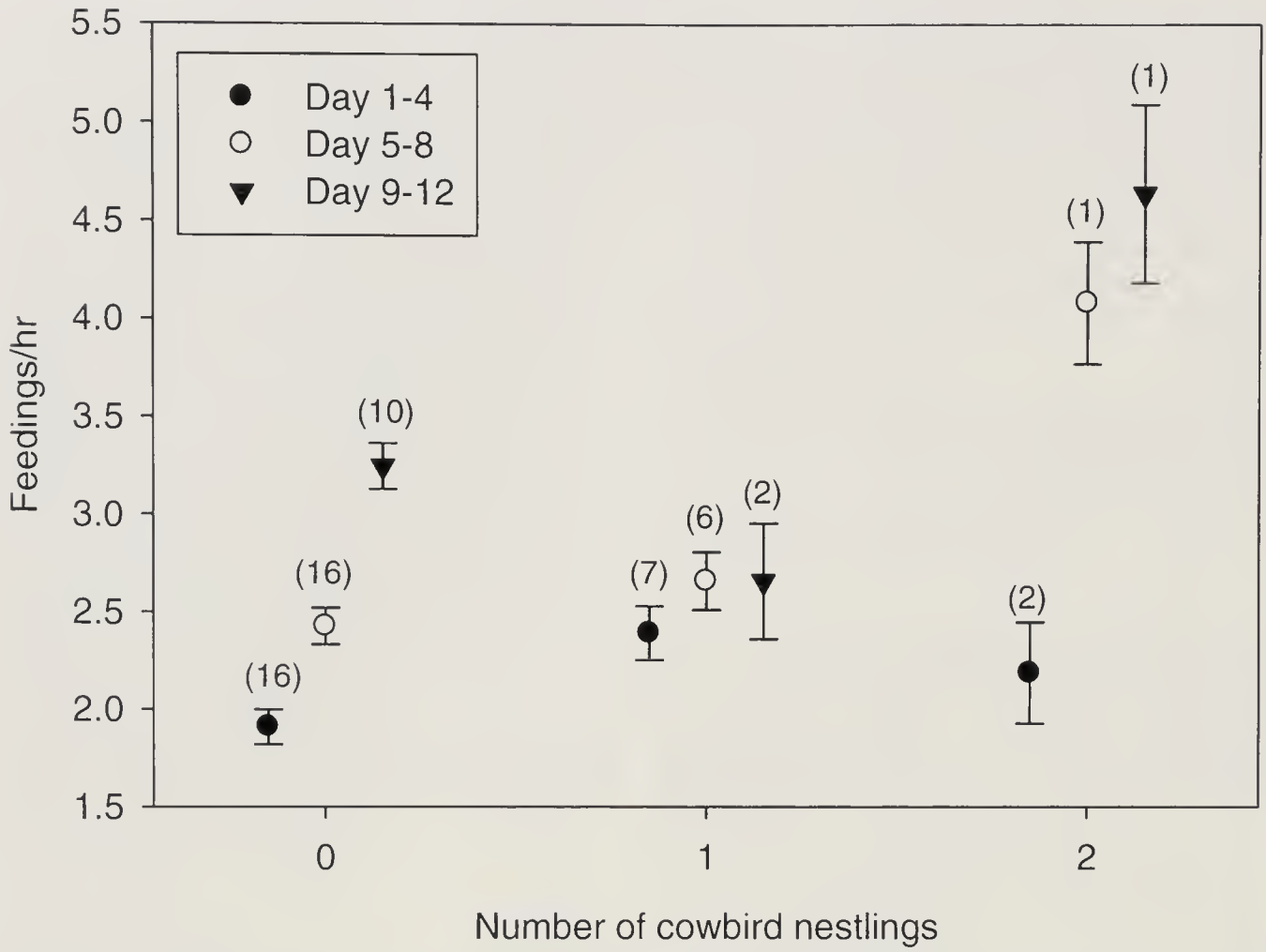

FIG. 2. Effects of Brown-headed Cowbird parasitism on provisioning rate (feedings/hr ± SE) at Swainson's Warbler nests during three different periods of the nestling stage. Values were calculated at the mean for brood size. Data were collected from 16 non-parasitized and nine parasitized nests at White River National Wildlife Refuge, Arkansas, 2006 and 2007. The sample size of nests for each category is in parentheses; most nests were observed at multiple states and do not equal sums of the total number of nests observed.

nestlings and those with two warblers and a cowbird nestling ($t = -2.76$, $P = 0.008$). There were no differences between nests with two warblers and those with a warbler and a cowbird nestling ($t = -0.87$, $P = 0.39$), or those with four warbler nestlings and those with three warblers and a cowbird nestling ($t = -0.35$, $P = 0.73$). Nests with two warbler nestlings or a warbler and a cowbird nestling had lower provisioning rates than those with two cowbird nestlings ($t = -3.75$, $P < 0.001$, and $t = -2.87$, $P = 0.007$, respectively). Nests with three warbler nestlings or two warblers and a cowbird nestling had similar provisioning rates to a nest with one warbler and two cowbird nestlings ($t = -1.19$, $P = 0.24$, and $t = 0.60$, $P = 0.55$, respectively).

The provisioning rate in nests that were not parasitized increased with nestling age ($t \geq 6.65$, $P < 0.001$; Fig. 2). There was a difference in provisioning rates between days 1 to 4 and 5 to 8 for nests with one cowbird nestling, ($t = -1.98$, $P = 0.050$), but no other combinations of two periods ($t \leq 0.92$, $P \geq 0.36$). A nest with two cowbird nestlings had a greater provisioning rate from days 5 to 12 than for days 1 through 4 ($t \geq 5.56$, $P < 0.001$), but rates for days 5 to 8 and 9 to 12 were similar ($t = -1.30$, $P = 0.19$). Nests with a single cowbird nestling during the early nestling period had greater provisioning rates than non-parasitized nests ($t = 2.88$, $P = 0.007$), but there were no differences between rates for nests with two versus no cowbirds ($t = 1.02$, $P = 0.32$), or for nests with one versus two cowbird nestlings during this stage ($t = 0.69$, $P = 0.49$). The frequency of parental feedings from days 5 through 8 was similar for non-parasitized nests and those with a single cowbird nestling ($t = -1.34$, $P = 0.19$), but both differed from a nest with two cowbirds ($t = -5.12$, $P < 0.001$, and $t = -4.17$, $P < 0.001$, respectively). The rate of provisioning during the late nestling period was marginally greater in non-parasitized when com-

pared to single-parasitized nests ($t = 1.85$, $P = 0.07$), but both differed from a double-parasitized nest ($t = -2.97$, $P = 0.004$, and $t = -3.65$, $P < 0.001$, respectively).

DISCUSSION

The effect of cowbird parasitism on the provisioning rate of Swainson's Warblers was variable and depended on brood size and age of nestlings. Our observed increases in provisioning rates with brood size for non-parasitized nests were consistent with trends observed for other species (e.g., Johnson and Best 1982, Haggerty 1992, Rosa and Murphy 1994), as were the results for increased provisioning to older nestlings (e.g., Johnson and Best 1982, Knapton 1984, Goodbred and Holmes 1996). These results were expected given the increasing energetic demand of each nestling as they grow (Williams and Prints 1986).

There were effects of parasitism on provisioning rates at nests with one to three nestlings, and for all three nestling-age categories. Differences were generally more pronounced for nests with two cowbird young. However, these results must be viewed with caution due to small sample sizes. We collected provisioning data from only two multiply parasitized nests, only one of those nests also contained a warbler nestling, and only one of the nests survived into the middle and late nestling periods. Similar effects of single and multiple parasitism have been observed for other species (Dearborn et al. 1998, Hoover and Reetz 2006). However, there appeared to be a limit to the provisioning rate for Swainson's Warblers. The mean provisioning rate of non-parasitized nests with four nestlings was similar to the rates for single-parasitized nests with three or four total nestlings (4 warblers vs. 2 warblers and 1 cowbird: $t_{60} = 1.08$, $P = 0.28$) and double-parasitized nests with two or three total nestlings ($t_{30} = 1.40$, $P = 0.17$; $t_{57} = 0.08$, $P = 0.94$, respectively). This similarity of mean rates among these brood sizes, given the larger size and begging intensity of cowbird nestlings (Dearborn 1998), suggests food may be a limiting factor (the mass of a cowbird at fledging is approximately twice that of an adult Swainson's Warbler; Lowther 1993, Brown and Dickson 1994, Hoover 2003).

The maximum observed clutch size for Swainson's Warblers at our study area was four eggs (Benson et al. 2010a). Our provisioning data support the hypothesis that this maximum is at least partly affected by food limitation (Lack 1947, 1954). The difference in productivity for Swainson's Warblers between successful non-parasitized (2.75 young/successful nest) and parasitized nests (0.60 young/successful nest) is among the more-extreme reductions in similar-sized passerines (Payne 1998). This reduction for Swainson's Warblers is mostly due to starvation of host nestlings (Benson et al. 2010a). The similar-sized Prothonotary Warbler (*Protonotaria citrea*), which breeds in lower elevation bottomland hardwood forests, is often able to fledge multiple cowbird and warbler young (Hoover 2003). The observed provisioning rates for Prothonotary Warblers ($\bar{x} = 9.54$/hr for non-parasitized, $\bar{x} = 16.96$/hr for parasitized nests; Hoover and Reetz 2006) far exceed the rates we observed for Swainson's Warblers ($\bar{x} < 5$/hr). Further evidence of food limitation of Swainson's Warblers in our study area includes food abundance which appears to influence habitat use (Brown 2008). These birds have larger home ranges than similar-sized passerines ($\bar{x} = 9.4$ ha; Anich et al. 2009), suggesting they require large areas to acquire necessary resources.

The increased sound and activity at parasitized nests has been observed to increase nest predation in some cases (Haskell 1994, Leech and Leonard 1997, Dearborn 1999, Tewksbury et al. 2002). Nest predation rates in our study population appeared to be unaffected by brood size or parasitism, possibly because predation rates were already relatively high (Benson et al. 2010a, b). However, the complex relationships among brood size, nestling age, parasitism status, and provisioning rate may lead to increased predation risk only in limited circumstances and not necessarily as a simple function of brood size or parasitism status.

We observed effects of parasitism on prey delivery rates by Swainson's Warblers, but several questions remain. For example, the size or type of prey that adults bring to the nest may differ among brood sizes or with nestling age in some species (Biermann and Sealy 1982), and the relative contributions of males and females to provisioning young may also vary (Nolan 1978, Carey 1990); these issues merit further study. The influence of habitat quality on provisioning rate and interaction between habitat quality and brood parasitism effects also remain unknown.

Habitat loss and fragmentation present significant conservation challenges for Swainson's Warbler populations. This fragmentation may

lead to low productivity due to high predation and brood parasitism rates in some populations (Benson et al. 2010a). Efforts should be made to conserve and improve existing habitats by providing forested buffers between quality Swainson's Warbler habitat and agricultural areas to reduce the negative effects of cowbird parasitism in this and other populations. Cowbird removal programs may be beneficial in limited circumstances, but are not cost-effective, or a permanent solution, and should be of secondary importance to habitat restoration and landscape-level management (Stutchbury 1997, Rothstein and Peer 2005).

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EFFECTS OF FAT AND LEAN BODY MASS ON MIGRATORY LANDBIRD STOPOVER DURATION

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ABSTRACT.—We used quantitative magnetic resonance body composition analysis and radiotelemetry to examine whether fat and lean body mass affected stopover durations of 11 birds captured during autumn migration in New York City, USA. Two Swainson's Thrushes (*Catharus ustulatus*), two Hermit Thrushes (*C. guttatus*), and seven Ovenbirds (*Seiurus aurocapilla*) were used in the study. Ovenbird stopover duration was significantly and negatively related to fat mass but unrelated to lean body mass. The same relationships were found when data from all three species were combined to increase sample sizes. Birds that departed within 1 day had fat stores upon capture that represented at least 11% of their total body mass whereas those with fat content <6% of total body mass remained for no fewer than 4 days. Arrival fat mass clearly influenced time birds spent at the site but lean body mass did not. Conditions for increasing or maintaining fat stores provided by urban stopover sites may affect the migration timing of birds. *Received 26 May 2009. Accepted 16 September 2009.*

Migrating landbirds require several stopovers for rest and refueling, as most are incapable of completing their migration in a single flight. Time and energy spent during stopover periods greatly exceeds that spent aloft (Wikelski et al. 2003, Bowlin et al. 2005), and behavior of birds at stopover sites can greatly influence their overall migration success. Factors that govern a bird's decision to terminate a stopover and begin the next flight have received much attention, particularly through development of theoretical models of optimal migration strategies (Alerstam and Hedenström 1998, Houston 1998). There is evidence that fuel stores, refueling rate, distance from final destination, date, predation risk, and weather conditions can individually, or in some combination influence a bird's length of stay at a given stopover site (Wang and Moore 1997, Åkesson and Hedenström 2000, Danhardt and Lindström 2001, Dierschke and Delingat 2001, Schaub et al. 2008).

Field studies of the effects of intrinsic and extrinsic factors on stopover duration are hampered by the difficulty of knowing when birds arrive at, and depart from, the site of interest. Several studies have measured stopover duration using mark-recapture data, while assuming birds were marked upon arrival and final recapture occurred on their actual departure date (e.g., Cherry 1982, Wang and Moore 1997, Morris and Glasgow 2001). The latter assumption can be especially tenuous, as migrants may learn to avoid mist nets (MacArthur and MacArthur 1974) or move beyond the coverage area within the stopover site (Chernetsov and Mukhin 2006, Tsvey et al. 2007). This method also relies on condition and behavior of the small proportion of birds that are recaptured to represent the majority, when recaptures may be biased towards individuals in poor condition that remain at the site for a relatively long time (Guglielmo et al. 2005, Morris et al. 2005, Hays 2008). More recently, survival analyses and other probabilistic models have been used to relax these assumptions and improve accuracy of stopover duration estimates based on mark-recapture data (Schaub et al. 2001, 2008), although large sample sizes are generally needed (Schaub 2006). Radio tracking offers another approach for measuring stopover duration that does not rely on recaptures and allows knowing departure date with near certainty (Chernetsov and Mukhin 2006, Tsvey et al. 2007). Drawbacks of radiotelemetry include high equipment costs, possible effects of transmitters on bird behavior, and the assumption that birds are captured upon arrival.

Examining the effect of energetic condition on stopover duration is complicated by the need for accurate, non-lethal measurements of body composition. Commonly used condition indices (e.g., body mass, size-corrected body mass, visual fat scores) can potentially provide reliable estimates of fat content (Conway et al. 1994, Spengler et al. 1995, Seewagen 2008). However, their accuracy may be species-specific (Skagen et al. 1993, Spengler et al. 1995, Seewagen 2008) or weak-

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ened by inter-observer variation (Krementz and Pendleton 1990), and they do not provide separate, direct measures of fat and lean body mass. Quantitative magnetic resonance analysis (QMR; Taicher et al. 2003, Tinsley et al. 2004) in contrast provides accurate, objective, and direct measures of the fat and lean body mass of small birds (CGG, unpubl. data).

We attached radio transmitters on 11 migrant songbirds at our study site in New York City during autumn 2008 in a pilot study to test the feasibility of radio tracking birds in an urban setting. We used a QMR body composition analyzer on all captured migrants for a concurrent study of body composition dynamics during stopover refueling. The stopover duration and body composition data obtained by radiotelemetry and QMR, respectively, afforded an additional opportunity to examine relationships between these variables. We coupled telemetry and QMR data to examine if arrival fat and lean body mass affected the stopover durations of these 11 migrants.

METHODS

Study Site and Animal Capture.—We captured birds during autumn 2008 on the grounds of the Bronx Zoo as part of an ongoing study of urban stopover ecology of migrant songbirds. The Bronx Zoo is a 107-ha park in Bronx County, New York, USA. Our study site was a 4.9-ha fragment of riparian forest on the eastern edge of the zoo that does not contain exhibits and is not open to visitors (40° 85′ N, 73° 87′ W). Red oak (*Quercus rubra*), sweet gum (*Liquidambar styraciflua*), swamp dogwood (*Cornus foemina*), and willows (*Salix* spp.) are the dominant tree species in the area. Previous research has suggested this site offers suitable refueling conditions for landbird migrants (Seewagen and Slayton 2008; CLS and CGG, unpubl. data).

Birds were captured in mist nets from sunrise until ~1200 hrs during 4 September to 22 October. Captured birds were marked with a U.S. Geological Survey aluminum leg band, measured (unflattened wing length to 1 mm), and weighed on a digital balance to 0.1 g. Approximately 75 µl of blood was collected by brachial veinipuncture for a separate study.

Magnetic Resonance Analysis.—Conscious birds were scanned within 45 min of capture and banding in a QMR body composition analyzer (Echo-MRI, Echo Medical Systems, Houston, TX, USA) housed in a customized mobile laboratory (Glendale Recreational Vehicles, Strathroy, ON, Canada) at the study site. Birds were scanned in duplicate on the "small bird" and "two-accumulation" settings of the Echo-MRI software, yielding measures of fat mass and wet lean body mass to 0.001 g. Total scanning time was ~4 min/individual and the average coefficient of variation for individual birds was 1.7% for fat and 0.4% for wet lean mass. Raw QMR scan data were transformed using calibration equations for small birds developed with House Sparrows (*Passer domesticus*) and Zebra Finches (*Taeniopygia guttata*) in a laboratory validation study (CGG, unpubl. data). Validation indicated the relative error for predictions of fat and wet lean mass were ± 11% and ± 1.5%, respectively.

Radiotelemetry.—We radiomarked each Swainson's Thrush (*Catharus ustulatus*), Hermit Thrush (*C. guttatus*), and Ovenbird (*Seiurus aurocapilla*) captured beginning 3 October until all 11 transmitters we had were deployed. These species were used because they are relatively common migrants in the area, body masses are amenable to radiotelemetry, and they are the focus of concurrent studies in progress at the site. The 0.5-g transmitters (A2415, Advanced Telemetry Systems, Isanti, MN, USA) were affixed after QMR scanning with eyelash adhesive directly to a cleared area of skin in the interscapular region (adapted from Raim 1978). Birds were held in bags for ~15 min to allow the adhesive to dry and released within 50 m of where originally captured.

We could not be certain birds were captured and marked upon arrival. Eight of 11 birds were marked on days when migrant capture rates were high (~double) relative to the 2 previous days at this site and at two affiliated banding stations elsewhere in New York City. This increased our confidence these individuals were new arrivals and marked during their first day at the stopover site (*sensu* Tsvey et al. 2007). However, we use the term "minimum stopover duration" hereafter because of this uncertainty.

We checked for presence/absence daily at sunrise, noon, and sunset using a handheld Yagi antenna and receiver (R4500S, Advanced Telemetry Systems, Isanti, MN, USA) from within the study site. We searched for birds from other points throughout the zoo including roofs of two three-story buildings if we initially failed to detect a signal from within the study site. We assumed

TABLE 1. Means ± SD and ranges of total body mass, fat mass, lean body mass, and minimum stopover durations of three species of migratory landbirds radiotracked during autumn stopovers in New York City, USA.

Species	*n*	Total body mass (g)	Fat mass (g)	Lean body mass (g)	Stopover duration (days)
Swainson's Thrush	2	27.3, 30.1	1.700, 2.410	22.760, 26.119	4, 5
Hermit Thrush	2	30.2, 34.6	1.570, 4.000	27.103, 29.089	2, 7
Ovenbird	7	20.0 ± 1.3	2.461 ± 1.069	17.009 ± 0.795	4.3 ± 5.0
		18.3–21.7	1.068–3.911	15.713–18.145	1–14

birds had left the area permanently and resumed migration if they were undetected for at least 4 consecutive days. We considered a stopover of 1 day as the initial capture of a bird at the site in the morning and departure any time that night.

Statistical Analyses.—We used standardized residuals from linear regressions of lean body mass and wing length to correct lean body mass for body size variation. We could not adjust fat mass in the same manner because fat mass was not significantly related to wing length. We instead divided fat mass by total body mass and arcsine-root transformed the proportions (Zar 1999, Gotelli and Ellison 2004).

We used backwards selection multiple regression with adjusted fat and lean body mass as predictor variables, and number of days of stopover as the response variable to examine the effect of body composition on stopover duration. Collinearity did not occur, as fat and lean body mass were not significantly correlated. We performed the analyses on Ovenbird data alone and on data from all three species combined.

Age and gender were not considered because sample sizes were small and not all birds could be confidently assigned to age or gender classes. All variables met normality assumptions. We conducted tests with SPSS 16.0 and interpreted results as significant when $P < 0.05$. Mean (± SD) values are reported.

RESULTS

We radiomarked two Swainson's Thrushes, two Hermit Thrushes, and seven Ovenbirds. Swainson's Thrushes were marked on 2 and 6 October, and Hermit Thrushes were marked on 10 and 11 October. Four Ovenbirds were marked on 3 October and three were marked on 6 October.

Minimum stopover durations ranged from 1 to 14 days (Table 1). Three individuals departed within 1 day and the remainder stayed for at least 2 days. Initial fat content ranged from 6 to 8% of total body mass in Swainson's Thrushes, from 5 to 12% in Hermit Thrushes, and from 6 to 18% in Ovenbirds. An Ovenbird was recaptured on the eighth day of its 14 day stopover; total body mass (measured by digital balance) increased 4.2 g (23% of original), and fat and lean body mass (measured by QMR) increased 2.767 g (259% of original) and 1.884 g (11% of original), respectively.

The initial fat loads of birds that stayed at the site for only 1–2 days ($n = 5$) averaged 14 ± 3% of total body mass, whereas the initial fat loads of birds that stayed for the longest periods (7, 8, and 14 days; $n = 3$) averaged 6 ± 0.5% of total body mass. Ovenbird stopover duration was unrelated to lean body mass ($r^2 = 0.02$, $F_{2,4} = 0.36$, $P = 0.58$), and significantly and negatively related to fat mass ($r^2 = 0.74$, $F_{1,5} = 13.95$, $P = 0.013$). The same relationships were found when data from all three species were combined to increase sample sizes (lean: $r^2 = 0.03$, $F_{2,8} = 0.00$, $P = 0.98$; fat: $r^2 = 0.56$, $F_{1,9} = 11.31$, $P = 0.008$; Fig. 1). The relationship between fat and stopover duration appeared non-linear, and we explored the fit of an exponential model to the data *a posteriori*. The exponential model was also highly significant ($r^2 = 0.71$, $F_{1,9} = 22.08$, $P = 0.001$; Fig. 1).

DISCUSSION

This is the first combination of magnetic resonance technology and radiotelemetry to examine the influence of fat and lean body mass on stopover duration to our knowledge. We believe this is also the first description of autumn stopover durations of migrants within a major urban center.

Fat mass upon presumed arrival date appeared to strongly influence how long birds remained at the stopover site. This is consistent with other findings that lean birds stop over longer than fatter birds (Cherry 1982, Loria and Moore 1990, Wang and Moore 1997, Matthews 2008; but see Safriel and Lavee 1988, Salewski and Schaub 2007). The

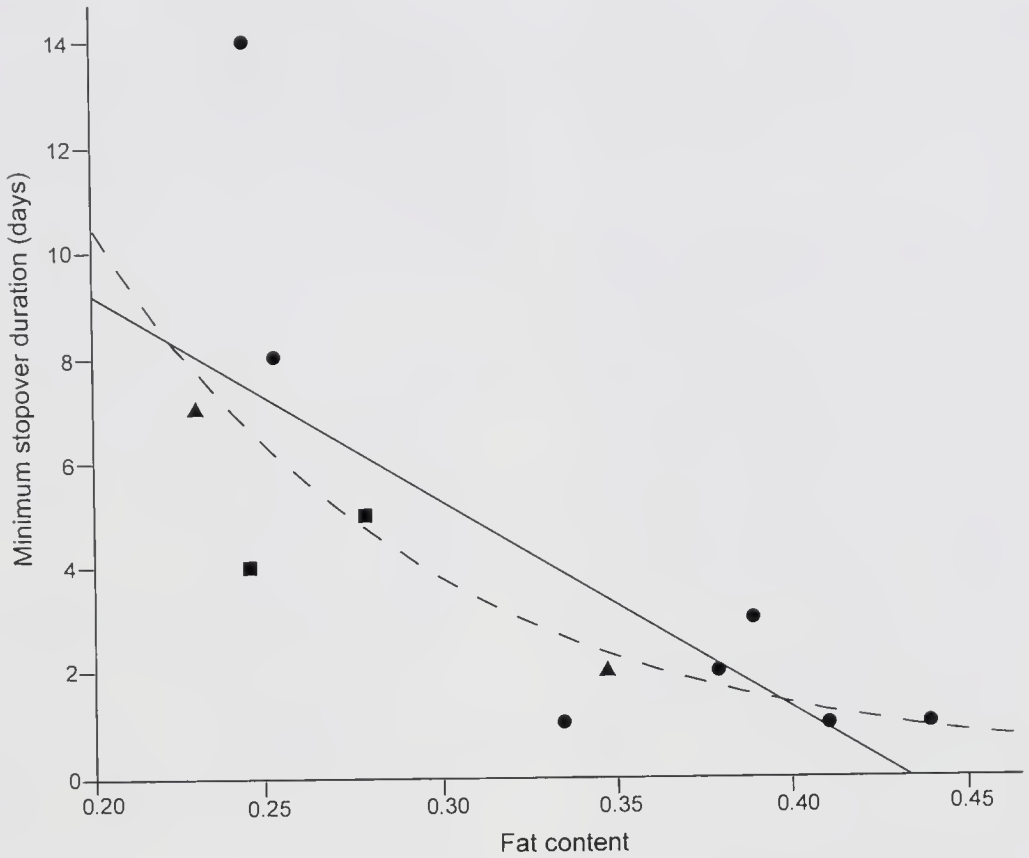

FIG. 1. Relationship between arrival fat content (arcsine-root transformed g fat/g total body mass) and minimum stopover duration of Swainson's Thrushes (squares), Hermit Thrushes (triangles), and Ovenbirds (circles) captured during autumn migration in New York City, USA. Solid and dashed lines represent linear ($r^2 = 0.56$, $F_{1,9} = 11.31$, $P = 0.008$) and exponential ($r^2 = 0.71$, $F_{1,9} = 22.08$, $P = 0.001$) models, respectively.

arrival fat content of individuals that stayed for only 1 day was at least 11% of total body mass, whereas all individuals with fat content <6% of total body mass remained for no fewer than 4 days, suggesting a possible threshold fat level for departure. However, how much additional fat birds acquired between capture and departure is unknown.

We did not find any relationship between lean body mass and minimum stopover duration. Lean tissues (e.g., flight muscles, digestive organs) may contribute significantly to total body mass dynamics during migration. This is particularly apparent in shorebirds that routinely make exceptionally long non-stop flights and in passerines when they must cross ecological barriers (Biebach 1998, Karasov and Pinshow 1998, Battley et al. 2000, Guglielmo and Williams 2003). No formidable ecological barriers exist immediately north of New York City, and it is possible most arriving autumn passerine migrants have not recently metabolized substantial non-fat tissue, and rebuilding of lean mass is not a significant component of stopover refueling. This is not supported by the lean mass gained by the recaptured Ovenbird which accounted for ~40% of its total body mass increase. Four of eight other (non-radio-marked) birds that we recaptured during the season also had gains in lean mass (CLS and CGG, unpubl. data). It is unknown from our small sample sizes of recaptured and radio-marked birds whether migrants commonly deposit lean tissue at this site and if lean body mass affects departure timing. Fusani et al. (2009) did not find lean mass (muscle scores) to influence migratory restlessness in two of three species examined. This also suggests lean mass does not influence departure decisions. Further study on the relationship between lean body mass and stopover duration is needed.

Fuel load is not the only variable that can influence stopover duration; weather, predation risk, and date are also factors that possibly govern a bird's decision to depart a stopover site. Our small sample size of 11 birds prohibited including additional predictor variables in the analyses and we cannot assess any effect they may have had on stopover duration. However, the birds were marked on 5 days over a span of only 9 days; thus, they probably experienced similar predation

risk and temporal pressure, and were exposed to comparable weather conditions. Arrival body composition likely differed among the individuals we studied more so than any of these potential extrinsic influences.

The recaptured Ovenbird may illustrate how multiple variables can affect stopover duration. This bird appeared to have stored sufficient fat to resume migration by its eighth stopover day, yet it remained at the site for 6 additional days. Overnight wind direction following recapture was primarily from the south until the night the bird departed when winds came from the north, the preferred direction of southbound passerines (Gauthreaux 1991). It is possible this bird was energetically prepared for departure by the eighth day but waited 6 additional days for more favorable overnight flying conditions. Six of the other birds similarly departed on nights with northern winds; the remaining four departed during eastern winds.

Our sample size was small, but arrival fat mass had a clear and strong effect on time birds remained at the stopover site. Similar relationships between stopover duration and some measure of energetic condition have been documented previously (Cherry 1982, Loria and Moore 1990, Wang and Moore 1997, Matthews 2008), but the contributions of fat and lean mass were not addressed individually. Quantitative magnetic resonance scanning allowed us to separately examine how each tissue affected stopover duration. Arrival fat mass at our study site affected migrants' decisions to leave whereas lean body mass did not. Thus, the conditions for increasing or maintaining fat stores provided by this site and possibly other similar urban habitats can affect the migration timing of birds using them. Our results demonstrate quantitative magnetic resonance analysis can be useful under field conditions, and that combining it with telemetry and other approaches will improve our ability to understand the stopover biology of birds.

ACKNOWLEDGMENTS

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SEASONAL FLUCTUATION OF THE ORANGE-WINGED AMAZON AT A ROOSTING SITE IN AMAZONIA

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ABSTRACT.—We recorded fluctuations in a population of Orange-winged Amazon (*Amazona amazonica*) during 1 year at a roosting site on an island near Belém, Pará, Brazil. Parrots were counted from a boat by a minimum of three teams of two observers, each team oriented in different directions. Orange-winged Amazons were observed flying alone (14.2%), in pairs (75.7%), and small numbers in family groups (pairs with young) of three (8.7%), four (1.2%), or five (0.3%) individuals. The larger number of groups of three compared with groups of four and five individuals reflects the low survival rate of nestlings with generally only one surviving offspring per brood. The total number of parrots increased from April (3,899) to July (8,539), and began to decrease in August (5,351). This decrease was presumably due to onset of the breeding season, when paired individuals leave the roost in search of a nest, where they breed, nest, and rear young until the nestlings can fly. *Received 24 January 2009. Accepted 28 August 2009.*

Temporal and spatial variations in estimates of wild animal populations are important indicators of underlying demographic processes and ecological interactions (Nunes and Betini 2002). Population estimates are particularly important in the case of parrots (Aves, Psittacidae) because this family has a disproportionate number of threatened species (Collar and Juniper 1992). Censusing over significant periods of time is an efficient tool to distinguish between natural and anthropogenic fluctuations (Bibby et al. 1992), which is essential for future conservation of species.

There are different methods to estimate population size of birds. In the case of parrots, most methods are based on counts of individuals by visual and/or auditory contacts (Collar and Juniper 1992). They are registered in high number early in the morning and late afternoon (Pizo et al. 1997), and counts in the middle of the day should be avoided because activity of parrots decreases abruptly at this time (Marsden 1999). Roost counts may permit targeted assessments of parrot populations in small areas and on islands where parrots roost communally (Snyder et al. 1987, Matuzak and Brightsmith 2007).

The Orange-winged Amazon (*Amazona amazonica*) gathers overnight in communal roosts (Sick 1997, Juniper and Parr 1998). Individuals meet just before or shortly after sunset (Sick 1997), making it relatively easy to obtain estimates of the minimum number of individuals (Nunes and Betini 2002). Our objective was to conduct population estimates of Orange-winged Amazons for all months of the year at a roosting site on the Ilha dos Papagaios (Parrot's Island), near Belém (Pará State, Brazil), discriminating family groups (single birds, pairs, and groups of three, four, or five individuals), and measuring seasonal fluctuation throughout the year.

METHODS

Study Area.—Ilha dos Papagaios is a roosting site for a significant Orange-winged Amazon population, a common species in the region. It is in Guajara Bay, south of Belém, Brazil (01° 31′ 37″ S, 48° 30′ 22″ W), and has an area of 7.4 ha, eight houses, and about 36 inhabitants. The island is low and subject to periodic tidal flooding (Novaes and Lima 1998). The climate is tropical humid and the source of the seasonality is the precipitation, although there is no pronounced dry season. There are two seasons: a rainy season and a less rainy season. The rainy season begins in December, peaks in March, and subsides in May. January, February, and March are the wettest months with average monthly rainfalls exceeding 400 mm. The less rainy season usually corresponds to the period from June to November, and October is the driest month with an average precipitation of 86 mm (annual precipitation = 2,800 mm; SECTAM 1994).

The vegetation is mostly dense alluvial forest with emergent and uniform canopy in areas of lowland floodplain. Flooded forests, and sandy alluvial deposits (beaches) covered by sparse vegetation, characteristic of Guajara Bay, are also present (Novaes and Lima 1998).

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Surveys.—Counts of *A. amazonica* were conducted at the roost on Ilha dos Papagaios. We conducted 96 surveys (54 in the afternoon and 42 in the morning) from September 2004 through September 2005. Parrots were counted from a single medium-sized boat (12 m long), positioned in a point (about 100 m southeast of the island) where it was possible to clearly observe all the main flight routes of the parrots' arrival and departure to and from the roost.

Two visits were made per week, one between 1700 and 1900 hrs and one the following day between 0500 and 0800 hrs, before sunset and sunrise, respectively. During counts, single birds, pairs, and groups of three, four, or five individuals were noted when possible with larger groups being counted or estimated when it was not possible to separate individuals.

Counts were made by three teams each with at least one observer and one auxiliary. Observers counted all individuals passing in their field of view, arriving or departing to or from previously selected directions in relation to the roost: (1) to or from the north and northeast of the island; (2) to or from the southeast and south of the island; and (3) parrots going to or arriving from the other side of the island. The teams were careful to not duplicate individuals already counted by themselves or by another team, eventually announcing loudly their counts to the near-by team. Each observer announced to his auxiliary the number and group composition of the parrots seen with the aid of 7 × 50 binoculars; the auxiliaries recorded these data on standardized forms, separating the numbers of birds seen per minute.

Statistical Analyses.—Data were analyzed with Statistica 7.1 software package (Stasoft Inc. 2005) and are expressed as means ± SD. Variables were examined for normality using Kolmogorov-Smirnov tests. All data followed a normal distribution and parametric tests were used (ANOVA and paired *t*-test). Differences between means were considered statistically significant at $P < 0.05$. We calculated the percentages of the parrot flocks flying to or from the roost (single birds, pairs and groups of three, four, or five individuals) per visit and averaged the data by month. Cluster analysis was conducted using the City-block (Manhattan) distance method and weighted pair-group average to test for seasonal differences (Sneath and Sokal 1973).

RESULTS

Patterns of Flight Behavior.—Single individuals (probably unpaired adults or young) accounted for 14.2 ± 6.7% of the observed groups, pairs (sexually mature adults) 75.7 ± 6.6%, and family groups of three (presumably pairs with 1 young) 8.7 ± 3.3%, groups of four (presumed pairs with 2 young) 1.2 ± 1.6%, and groups of five (presumed pairs with 3 young) 0.3 ± 0.4%.

Total Number of Individuals and Seasonal Fluctuation.—The average number of individuals per visit varied by month (Fig. 1). June (7,084 ± 1,708) and July (8,539 ± 704) had the highest number of parrots counted at the roosting site (max = 9,603 on 2 July 2005). Total numbers decreased in August (5,351 ± 1,534) and again in September (3,819 ± 462 in 2005 but only 2.040 ± 383 in 2004). The lowest counts were recorded from October (1,545 ± 245) through December (1,364 ± 161), followed by a slightly higher level in January (1,895 ± 223), February (1,778 ± 356), and March (2,361 ± 453), after which the number increased steadily (3,899 ± 547 in April and 4,484 ± 814 in May) until the July peak.

Size of Flocks and Seasonal Fluctuation.—The number of single individuals, pairs, and groups of three, four, and five individuals varied over the year (Fig. 2). These patterns were similar to those for total numbers, except for groups of four and five individuals, which were essentially absent from September until December. In January 2005 they began to increase, reaching a level of ~3.5 and ~2.3%, respectively between March and July 2005, and then decreased in August and September 2005.

Annual Cycle.—Monthly values separated into three major groups (Fig. 3). The first period included September 2004 to March 2005, the second period was April, May, August, and September 2005, and the third period was June and July 2005.

There was a significant difference between these periods in total number of parrots across all flock sizes (ANOVA $F_{2,92\text{total}} = 339.96$, $P < 0.01$; $F_{2,92\text{single}} = 37.15$, $P < 0.01$; $F_{2,92\text{pairs}} = 204.51$, $P < 0.01$; $F_{2,92\text{three}} = 152.55$, $P < 0.01$; $F_{2,92\text{four}} = 36.58$, $P < 0.01$; $F_{2,92\text{five}} = 18.80$, $P < 0.01$) (Table 1).

All comparisons of total number and number of single individuals, pairs, and groups of three, were significant: the averages for period 1 were smaller than those for period 2, which were smaller than those for period 3. Total numbers of parrots and

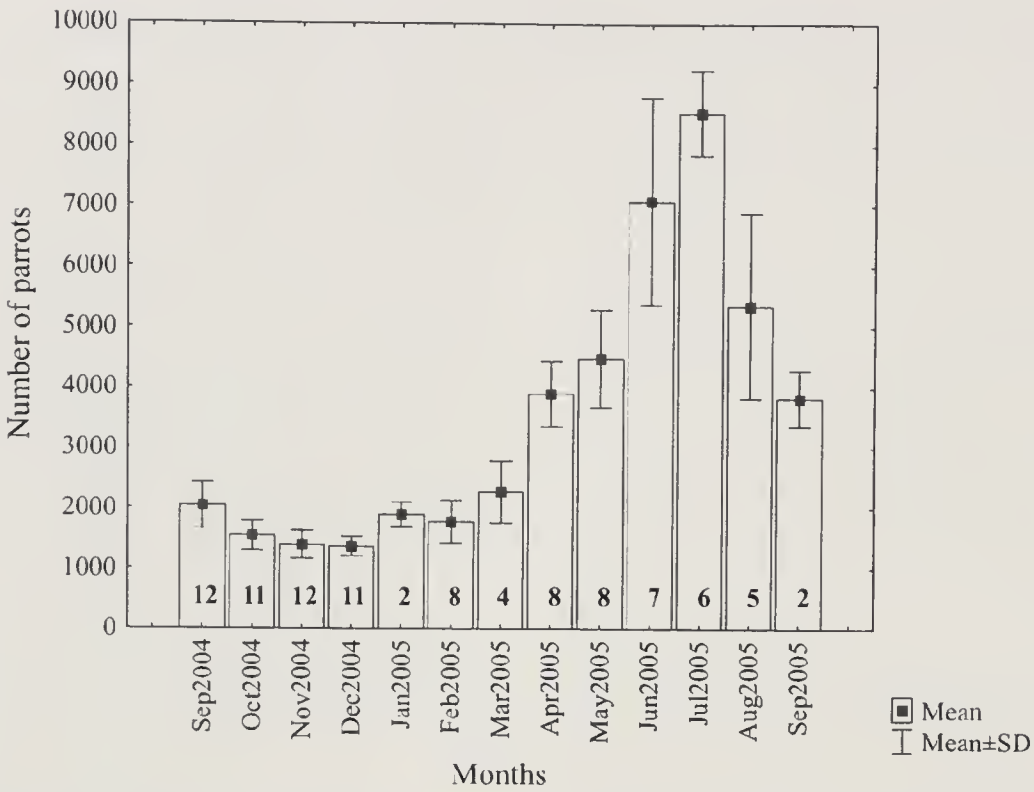

FIG. 1. Number of roosting Orange-winged Amazons by month. Number of counts (*n*) is inserted in the respective column.

numbers of single individuals, pairs, and groups of three in 2005 increased significantly from April with a new significant increase in June and a significant decrease after August. Only period 1 versus 2 and period 1 versus 3 were significantly different in the case of groups of four and five individuals.

Validation of Counts.—The number of parrots that arrive at the roosting site in the evening should be related to the number that leave the following morning. We verified the reliability of our counts by comparing the average number of parrots arriving with the average number leaving the roost using a paired *t*-test. We used the average total number of parrots in each of the three significantly different periods previously identified (Fig. 3). Differences between afternoon and morning averages were not significant (from Sep 2004 to Mar 2005: afternoon = 1,662 ± 364 vs. morning = 1,597 ± 438, $t_{21} = 0.81$, $P = 0.43$; Apr, May, Aug, and Sep 2005: afternoon = 4,110 ± 824 vs. morning = 4,571 ± 995, $t_9 = 1.46$, $P = 0.62$; Jun and Jul 2005: afternoon = 8,080 ± 1,394 vs. morning = 8,122 ± 1,399, $t_6 = 1.52$, $P = 0.18$).

DISCUSSION

Counting Method.—The method used in this study of counting parrots from a fixed site as they arrived at or left the roost is similar to that used by other parrot researchers who have studied other parrot species (Rocha et al. 1988, Guedes 1993, Casagrande and Beissinger 1997, Mabb 1997, Martinez and Prestes 2002, Harms and Eberhard 2003, Cougill and Marsden 2004, Berg and Angel 2006, Costa 2006, Matuzak and Brightsmith 2007). Some parrots could have arrived at or left the island by routes not countable from the survey boat. Thus, our technique provides only a minimum of the number of individuals at the roost (Nunes and Betini 2002). We did not find a significant difference between the number of parrots that arrived and the number that left the roosting site and we can consider our counts valid.

Number of Individuals, Seasonal Fluctuation, and Breeding Season.—The breeding season is apparently a primary factor influencing the fluctuation in number of parrots at the roosting site throughout the year. Nesting female parrots cannot roost gregariously if they are to incubate eggs and take care of offspring (Berg and Angel 2006). It is common that numbers of parrots at roosting sites diminish during the period when pairs need to find nest sites, lay, and incubate eggs (Cannon 1984, Chapman et al. 1989, Carrillo et al. 2002). These findings are similar to those reported for other species of parrots (Mabb 1997, Olmos 1997, Berg and Angel 2006, Costa 2006, Matuzak and Brightsmith 2007); however, the period of low attendance at the roost is particularly long at our study site.

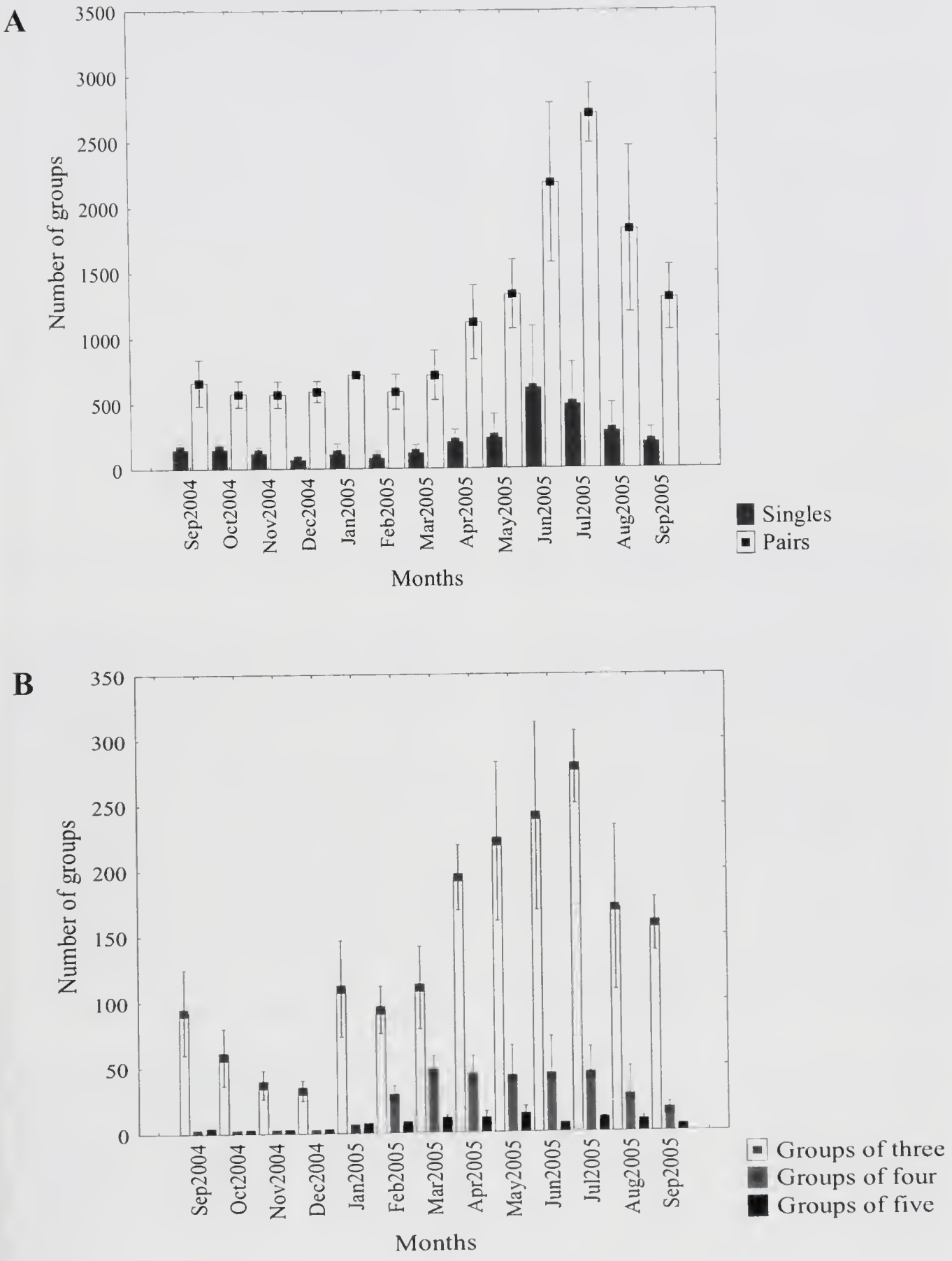

FIG. 2. Number of roosting flocks of Orange-winged Amazons by month. (A). Single birds and pairs. (B). Groups of three, four, and five individuals.

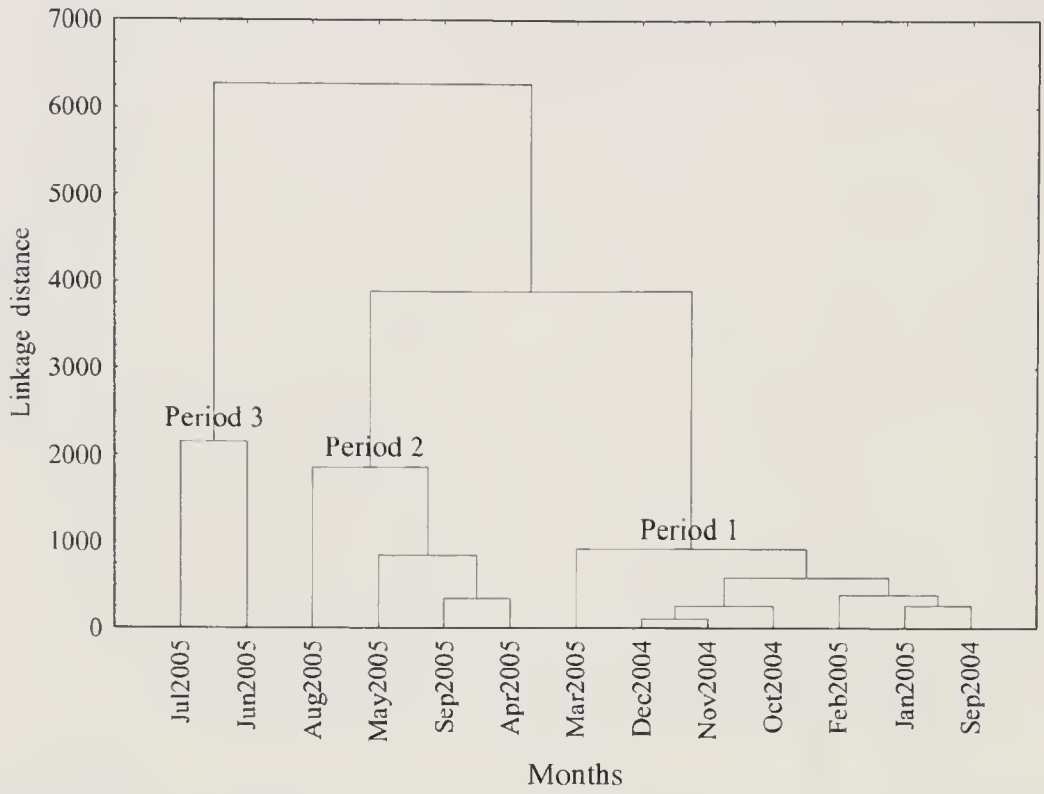

FIG. 3. Tree-clustering of monthly average values of total number of Orange-winged Amazons and number in each grouping (single birds, pairs, groups of three, four, and five individuals) per visit.

Orange-winged Amazons have asynchronous reproduction that may account for the long time between the decrease of the roost population and the return of pairs with young. Parrots began to leave the roost in August and their dispersal was completed by October, while pairs started to come back to the roost with their young in January (Fig. 2). Other parrots are still breeding at this same time, and it is only in June, when other nestlings had become emancipated from their parents, that number of individuals reached its yearly maximum.

Patterns of Flight Behavior.—Parrots in the genus *Amazona* remain in family groups even when flying and roosting in larger aggregations, and such groups are easily recognizable (Martuscelli 1995). Most parrots flew in pairs during the counts, which is the primary social unit at least for Amazons, as they are monogamous and pair for life (Snyder et al. 1987, Sick 1997, Gilardi and Munn 1998, Juniper and Parr 1998, Guedes and Seixas 2002). Single individuals (14.2% of group occurrences) are probably unpaired adults or young that have not reached sexual maturity but are no longer accompanied by their parents. Young remain with their parents only until the parents began to nest again (Sick 1997).

Groups of three constituted 8.7% of all groups, groups of four 1.2%, and groups of five 0.3%, suggesting small family groups (Gilardi and Munn

TABLE 1. Size of flocks of Orange-winged Amazons at an Amazonia roosting site, Brazil, 2004–2005 (cluster analysis using Tukey's HSD test).

Comparison	Total number	Single birds	Pairs	Goups of three	Goups of four	Goups of five
Period 1 vs.	1678 ± 422	118 ± 53	610 ± 128	66 ± 35	7 ± 14	2 ± 3
Period 2	4411 ± 1035	230 ± 153	1363 ± 443	196 ± 51	36 ± 22	8 ± 7
P – value	<0.01	<0.05	<0.01	<0.01	<0.01	<0.01
Period 1 vs.	1678 ± 422	118 ± 53	610 ± 128	66 ± 35	7 ± 14	2 ± 3
Period 3	7755 ± 1495	557 ± 397	2430 ± 532	259 ± 57	43 ± 26	6 ± 3
P – value	<0.01	<0.01	<0.01	<0.01	<0.01	<0.05
Period 2 vs.	4411 ± 1035	230 ± 153	1363 ± 443	196 ± 51	36 ± 22	8 ± 7
Period 3	7755 ± 1495	557 ± 397	2430 ± 532	259 ± 57	43 ± 26	6 ± 3
P – value	<0.01	<0.01	<0.01	<0.01	>0.05	>0.05

1998). The higher number of groups of three (presumably pairs with one young), compared with groups of four and five individuals (presumed pairs with 2 and 3 young, respectively), reflects the characteristically low survival rate of nestling parrots (Gnam and Rockwell 1991, Munn 1992, Guedes 1993, Lindsey et al. 1994, Carrillo et al. 2002, Seixas and Mourão 2002). We observed clutches of 2–4 eggs in five nests, but only one nestling survived in each of the two nests that were not visited for the illegal pet trade (Moura et al. 2008) when we studied reproductive biology of the Orange-winged Amazon during the 2006/2007 breeding season in Santa Bárbara (Pará State, 41 km from the roosting site).

Orange-winged Amazons have a wide distribution and are usually abundant and, at the moment, are not at risk (BirdLife International 2008). However, this species is largely captured from the wild for the international trade in Brazil, being fourth on the list of most apprehended species of parrots by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) (Oliveira and Caparroz 2007). It is a popular, although illegal, pet in the region and poaching is intensive. Thus, it is important to monitor Orange-winged Amazon populations for effective conservation actions in the future.

Ilha dos Papagaios should be considered a priority area for conservation as it is an important refuge for the parrots. It is close to an urban center (8 km from Belém, population of 2-million inhabitants) and is a convenient site for environmental education programs, where people can see a great number of free parrots and become aware that the strong culture of having a wild bird as pet is a crime against nature.

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COSTS AND BENEFITS OF FORAGING ALONE OR IN MIXED-SPECIES AGGREGATIONS FOR FORSTER'S TERNS

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ABSTRACT.—Forster's Terns (*Sterna forsteri*) often forage alone or within mixed- species foraging aggregations. We investigated the relative costs and benefits of these two foraging strategies. Metrics used to assess differences in strategies included the number of attempts for prey (both successful and missed), capture efficiency, and capture rate. Forster's Terns foraging socially cue on presence and behavior of other aggregating species, especially Snowy Egrets (*Egretta thula*). Joining aggregations significantly increased their capture rate, but not their capture efficiency, compared to solitarily foraging terns. However, total aggregation size, influenced primarily by the two most abundant species, Laughing Gulls (*Larus atricilla*) and Snowy Egrets, affected tern behavior. For example, diving terns often collided with Laughing Gulls, causing frequent missed attempts for socially foraging individuals. Thus, large aggregation sizes had a negative effect on foraging success, perhaps because of interference and/or prey depletion. In contrast, solitarily foraging terns dove less often for prey but also missed less often. This may be why terns were observed foraging solitarily as aggregation sizes and congestion increased. *Received 20 February 2009. Accepted 17 July 2009.*

Important among an individual's behavioral decisions are those regarding food acquisition. Each individual must decide when and where to forage (Charnov 1976), on what prey item(s) to focus (Schoener 1971, Collier et al. 1991), and what capture strategy to use (Ydenberg et al. 1994). These decisions are constrained by the necessity of energy acquisition and will ultimately influence an animal's fitness.

One option animals can choose to make food acquisition decisions easier is to join a group in a process called local enhancement. Foraging in groups has been shown to provide benefits, including reduction of an individual's energy intake variance (Caraco 1981), increased prey capture rate (Pulliam and Millikan 1982), reduced energy expenditure (Master et al. 1993), increased vigilance (Caldwell 1986), reduced predation risk from "many-eyes" (Lima 1995) or dilution effects (Hamilton 1971), and the imparting of information about novel foraging techniques (Webster and Lefebvre 2001). Foraging in a group also has disadvantages, including increased conspicuousness to predators (Hamilton 1971, Bertram 1978, Caldwell 1986) and increased energy expenditure on aggressive interactions with competing foragers (Grand and Dill 1999).

Some disadvantages of feeding within a group may be assuaged if individuals join mixed rather than single-species groups to forage. The competitive costs of food acquisition are, at times, reduced by species-specific preferences for prey items in mixed-species feeding aggregations among wading birds (Moreno et al. 2005). Competitive costs are also moderated by differences in preferred feeding locations (Moreno et al. 2005) and by reduced interference due to variation in prey catching techniques (Latta and Wunderle 1996).

Few studies of Forster's Tern (*Sterna forsteri*) foraging behavior have been conducted (but see Salt and Willard 1971, Reed 1985). We investigated tern feeding behavior within mixed-species aggregations of wading birds and while foraging solitarily in a salt marsh in southern New Jersey, USA. Our goals were to: (1) identify the role of terns in formation and structure of mixed-species aggregations that progress from an initial "formation phase" with few species and individuals to an active phase with more species and individuals, and finally to a dispersal phase (Master et al. 1993); and (2) investigate foraging tactics used by terns under changing social conditions by comparing benefits accrued versus costs incurred by feeding within aggregations and solitarily.

METHODS

Study Area.—This study was conducted over two summer seasons (2004–2005) in a 2,083-ha salt marsh in southeastern New Jersey, USA (~39° 3′ N, 74° 46′ W). This marsh provided an unusually large number of relatively shallow (~3–60 cm) pools in which terns forage (Master 1992). The majority of fish prey within the pools were mummichogs (*Fundulus heteroclitus*) and

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sheepshead minnows (*Cyprinodon variegatus*); prey density averaged (± SD) 147.15 ± 57.92 fish/m^2 in the pools (Master 1992). The population of Forster's Terns in southern New Jersey was estimated at 403 individuals in the late 1970s and early 1980s (Spendelow and Patton 1988). At least eight separate colonies were within Cape May County more recently although numbers of birds were not reported (Walsh et al. 1999).

Foraging Observations.—Terns were observed from June until mid-August during each field season. Both solitary and aggregated terns were observed using binoculars (Nikon 10 × 40) or a spotting scope (KOWA TSN 821, 20–60× zoom), depending on the subject's proximity to the observer. We defined a mixed-species aggregation as a group of at least four birds from at least two different species foraging within close proximity (~1 m) to one another at a single pool. The species most often composing aggregations, in addition to terns, were Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), Glossy Ibis (*Plegadis falcinellus*), Great Blue Heron (*Ardea herodias*), Laughing Gull (*Larus atricilla*), and Least Tern (*Sterna antillarium*). Aggregations ranged in size from four to 430 individuals (mean aggregation size ± SE: 93.74 ± 4.70, $n = 87$).

Observations began each morning at sunrise as aggregations were forming and continued until ~1130 hrs EDT, when nearly all aggregations had dispersed. An aggregation was chosen randomly at sunrise and the total number of species represented and number of individuals of each species were counted. Numbers of individuals were summed to calculate total aggregation size. A single Forster's Tern was selected for observation, after the initial count, using the focal animal sampling technique (Schmitz and Baldassarre 1992). The focal tern was observed for 7 min (Balph and Romesburg 1986, Rooney and Sleeman 1998) during which the number of successful and missed foraging attempts was recorded. Capture rate and capture efficiency were calculated from these observations by dividing the number of successful attempts by the observation time of 7 min, and by dividing the number of successful attempts by the total number of attempts, both successful and missed, respectively.

A 10-min intermission followed observation of a focal individual prior to the next 7-min observation to allow terns to re-distribute themselves throughout the aggregation. After the intermission, a second count of the participants in the aggregation was recorded, another tern was selected, and a 7-min focal observation was begun. Our protocol continued in this manner for 58 min, providing four separate focal tern observations and species counts per aggregation (3 10-min intermissions between 4 7-min observation periods). Additional aggregations were located for continued observation until the ~1130 hrs dispersion time. The Schmitz and Baldassarre (1992) sampling procedure does not ensure an individual tern is observed only once, but this procedure is well accepted when studying aggregating animals and is resistant to potential sampling biases (Weinstein 1995). There were 38 aggregations studied in 2004 and 49 in 2005. Observations were conducted on 275 focal terns (126 in 2004 and 149 in 2005).

Observations were also conducted on terns foraging solitarily. These observations followed a similar protocol with two exceptions. First, aggregation counts were unnecessary. Second, solitary terns were observed for as long as they were visible. Nineteen solitary terns were observed with a mean (± SD) observation time of 7.00 ± 1.09 min. Total attempts, capture rates, and capture efficiencies were calculated on a per 7-min basis for comparison with aggregating terns. Solitary terns were observed during the same morning period as aggregations (sunrise to ~1130 hrs).

Data Analyses.—Each focal tern and the corresponding aggregation survey were treated as independent samples throughout the data analyses, ($n = 275$), rather than considering each aggregation with four individual terns as an independent sample ($n = 87$). This methodology was justified as intermission periods between observations allowed terns to redistribute themselves randomly throughout the space above a pool providing for unbiased observation of foraging birds. Observations of focal individuals can be considered independent if the time lag between observations is sufficient for an animal to traverse its range (Swihart and Slade 1985, Minta 1992). The 10-min interval between tern observations was sufficient for a tern to traverse the space above a pool. This also provided us with a precise time of day and aggregation size for each focal bird. Analyses using each tern and corresponding survey as independent samples were compared to analyses in which one tern and one survey from each aggregation were randomly selected for analysis. The results of these random selections were similar in all cases with those using all four focal individuals from a single

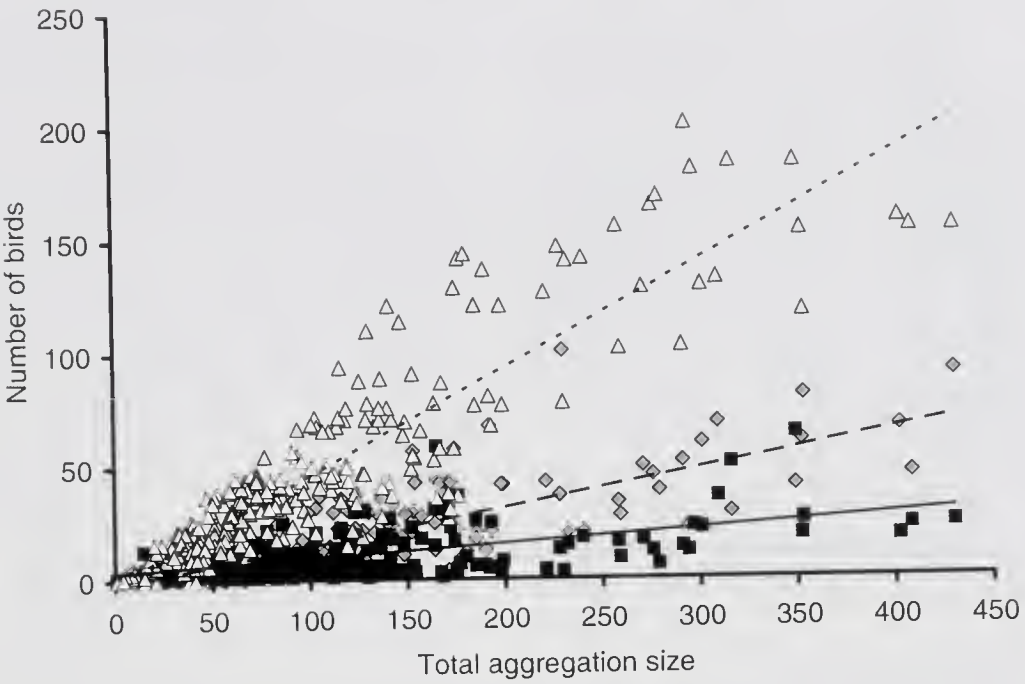

FIG. 1. Numbers of Laughing Gulls (open pyramids, dotted line), Snowy Egrets (shaded diamonds, dashed line), and Forster's Terns (dark boxes, solid line) by aggregation size. The number of gulls (slope = 0.48) and egrets (slope = 0.17) increased faster than the number of terns (slope = 0.06) as group size increased.

aggregation (Pearson product-moment correlation, $r = 0.99$). Observations were separated into four time intervals: dawn until 0630, 0631–0730, 0731–0830, and 0831 hrs EDT until dispersal. Group sizes were divided into four categories: solitary terns; and aggregations with 4 to 50, 51 to 100, and >100 birds. The data were then analyzed using two-factor completely randomized ANOVAs.

RESULTS

Aggregation Characteristics.—Forster's Terns were often observed foraging within aggregations. Laughing Gulls (44% of the total birds within a group), Snowy Egrets (15%), and terns (12%) were the three most abundant species, respectively, in these groups. Total aggregation size was most significantly influenced by number of Laughing Gulls ($\beta = 0.60$), followed by Snowy Egrets ($\beta = 0.38$), and Forster's Terns ($\beta = 0.20$; stepwise multiple regression: $F_{3,272} = 1693.95$, $P < 0.0001$, $r^2 = 0.95$; Fig. 1). The number of terns in aggregations increased with total aggregation size, but number of terns in these groups increased more slowly compared to the number of gulls and egrets. Thus, the proportion of total aggregation size comprised by terns decreased with increasing group size ($F_{1,274} = 33.93$, $P < 0.01$, $r^2 = 0.11$, $\beta = -0.33$).

The number of terns participating in feeding aggregations was influenced not only by total aggregation size, but by time of day (one-way ANOVA on tern number across the 4 time intervals: $F_{3,272} = 2.964$, $P = 0.03$). Terns were most numerous in aggregations during the early morning periods from sunrise until 0730 hrs (mean number of terns in aggregations ± SE: 10.58 ± 1.17 from sunrise to 0630, 10.11 ± 1.01 from 0631–0730) with mean numbers declining significantly throughout the remainder of the morning to 7.72 ± 0.75 during the 0731–0830 period, and to 5.73 ± 0.99 during the 0831-dispersal time period (*ad hoc* linear comparison within the ANOVA: $F_{1,272} = 7.798$, $P < 0.01$).

The contribution that terns made to aggregations was most substantial during the formative period of the aggregation but then declined (one-way ANOVA: $F_{3,272} = 2.55$, $P = 0.05$). Forster's Terns comprised a high percentage of aggregations initially (18.43 ± 2.48%), followed by a decline for the rest of the aggregation's existence (12.44 ± 1.44% for 0631–0730; 12.43 ± 1.20% for 0731–0830; 13.66 ± 0.38% for 0831-dispersal). Rather than a linear decline (*ad hoc* linear comparison within the ANOVA: $F_{1,272} = 1.88$, $P = 0.17$), the percentage of terns in aggregations was initially high and then decreased to a relatively stable lower level until aggregation dissolution (comparison of initial vs. other 3 intervals: $F_{1,272} = 6.38$, $P = 0.01$).

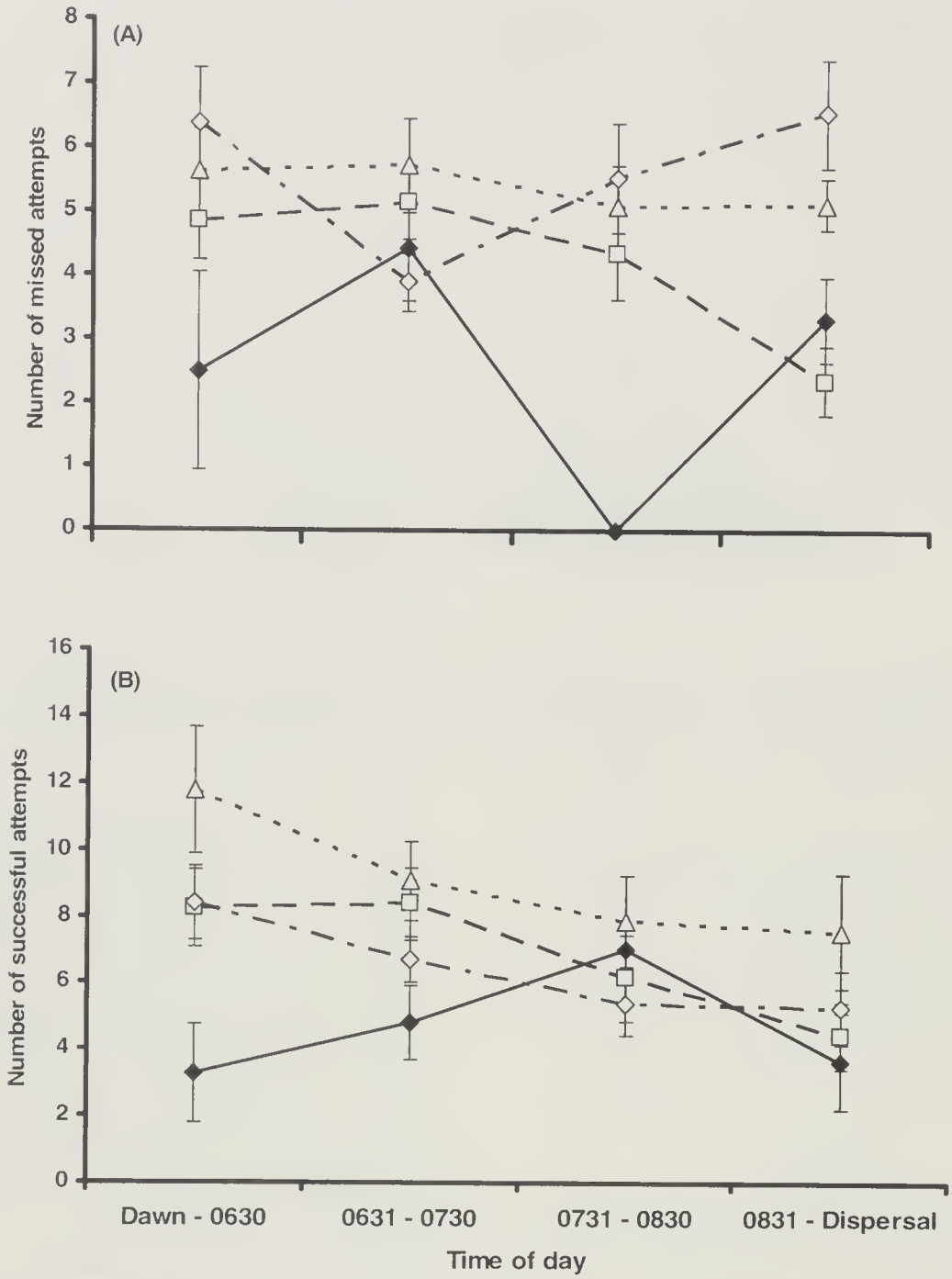

FIG. 2. Mean (± SE) number of (A) missed and (B) successful attempts over time by Forster's Terns foraging solitarily (dark diamonds, solid line) and within aggregations of: 4 to 50 birds (open boxes, dashed line), 51 to 100 birds (open pyramids, dotted line), and >100 birds (open diamonds, variably dashed line).

Foraging Strategies.—Both aggregated and solitary terns frequently dove into pools to capture prey; however, many of their attempts missed. Solitary birds tended to make fewer dives overall than aggregated birds and therefore missed prey less often than aggregated birds (aggregation size effect within the two-way ANOVA: $F_{3,273} = 4.078$, $P = 0.007$; Fig. 2A). The number of missed attempts did not change significantly for all birds over time (time of day effect within the two-way ANOVA: $F_{3,273} = 0.500$, $P = 0.687$), but there was a significant interaction between aggregation size and time of day ($F_{3,273} = 1.928$, $P = 0.048$). Solitary birds tended to miss capture of prey less than aggregated birds. Terns in small (4 to 50 total individuals) to moderate-sized (51 to 100) groups missed more often than solitary birds but less often than birds in large aggregations (>100 birds) and missed more often early in the morning than later (linear trend comparison within the ANOVA: $F_{1,273} = 8.562$, $P = 0.004$). Terns in large congested aggregations frequently missed prey continuing throughout the morning. Occasional collisions with competitors,

especially Laughing Gulls, may have been at least partially responsible for misses by terns in aggregations.

The number of times that terns were successful in capturing prey during dives was also influenced by group size (aggregation size effect within the two-way ANOVA: $F_{3,273} = 3.239$, $P = 0.023$; Fig. 2B). Solitary terns overall dove relatively infrequently and had the fewest successful dives. Terns in small or moderate-sized aggregations were most successful, while terns in large aggregations made comparatively few successful dives (quadratic trend comparison of group size within the ANOVA: $F_{1,273} = 4.673$, $P = 0.031$). The number of successful dives by terns in aggregations appeared to decline throughout the morning, but the trend was not significant (time of day effect within the two-way ANOVA: $F_{3,273} = 1.234$, $P = 0.298$), nor was the interaction between time of day and group size ($F_{9,273} = 0.430$, $P = 0.918$).

Terns in aggregations, as a result of diving more frequently, had higher capture rates than solitary terns (aggregation size effect within the two-way ANOVA: $F_{3,273} = 3.197$, $P = 0.024$; Fig. 3A). However, aggregated terns had fewer successful dives later in the day, causing their capture rates to decline throughout the morning (linear trend comparison within the ANOVA: $F_{1,273} = 9.341$, $P = 0.002$), while capture rates for solitary birds did not (time of day effect within the two-way ANOVA: $F_{3,273} = 1.463$, $P = 0.225$; interaction between time of day and group size: $F_{9,273} = 0.338$, $P = 0.962$).

Capture rates differed for the two strategies, but capture efficiency was similar for aggregated and solitarily foraging terns (aggregation size effect within the two-way ANOVA: $F_{3,273} = 1.414$, $P = 0.239$; Fig. 3B). The capture efficiency for solitary birds appeared more variable than for aggregated birds throughout the morning, but there were no significant differences in either time of day for all birds ($F_{3,273} = 2.225$, $P = 0.086$) or the interaction between group size and time ($F_{9,273} = 1.478$, $P = 0.156$).

DISCUSSION

Forster's Terns were frequent participants within aggregations, contributing significantly to the overall size of these mixed-species groups. Terns were less numerous in aggregations than either Snowy Egrets or Laughing Gulls and, as mornings progressed and more of these birds joined aggregations, the terns left.

These observations likely reflect the foraging strategy of terns relative to wading birds that comprised these large, congested aggregations. The presence of birds at a pool during the early morning formative period indicated to searching terns that it was a worthwhile patch to exploit (Armstrong 1970, Master 1992). Foraging maneuvers of wading birds, especially near the shoreline of pools, serve to flush prey into open water (Kushlan 1978). This maneuvering, particularly by the actively foraging Snowy Egrets, has been shown to enhance capture opportunities for other wading birds in the group (Russell 1978), and apparently for Forster's Terns.

Terns used a "hover-hunt" technique over the center of the pool, after prey had been flushed. In this behavior, terns would actively beat their wings to remain stationary in the air ~7 to 10 m above the center of the pool's surface. A tern would then dive into the water to capture a fish and, if successful, would fly across the pool while swallowing its prey until returning to its hovering position. If unsuccessful, the bird would return to its hovering position. Hover hunting was most successful for terns early in the morning, when both their number of successful dive attempts and rates of prey capture were highest. These results seem intuitive as, during this time of the morning, prey has been beaten from cover but are still abundant while competing foragers are still low in number. The total number and proportion of terns in aggregations increased during the formative period reflecting good foraging conditions. This technique became less successful as time progressed and aggregations grew in size, prey density declined and other birds became obstacles during diving, reducing both the terns' number of successful attempts and capture rates. Previous studies have shown that foraging activity of aggregations does impact pool fish populations by reducing density by 80% on average (Master 1992). Solitary terns, in contrast to aggregated terns, used a "circle hunt" behavior consisting of flying a circle around the perimeter of the pool at a relatively low height of 1 to 3 m. The tern would dive into the water after spotting a prey item. Whether successful or not, the bird would rise from the water and continue its circling flight until diving again or leaving the pool. This behavior likely flushed some prey items, but

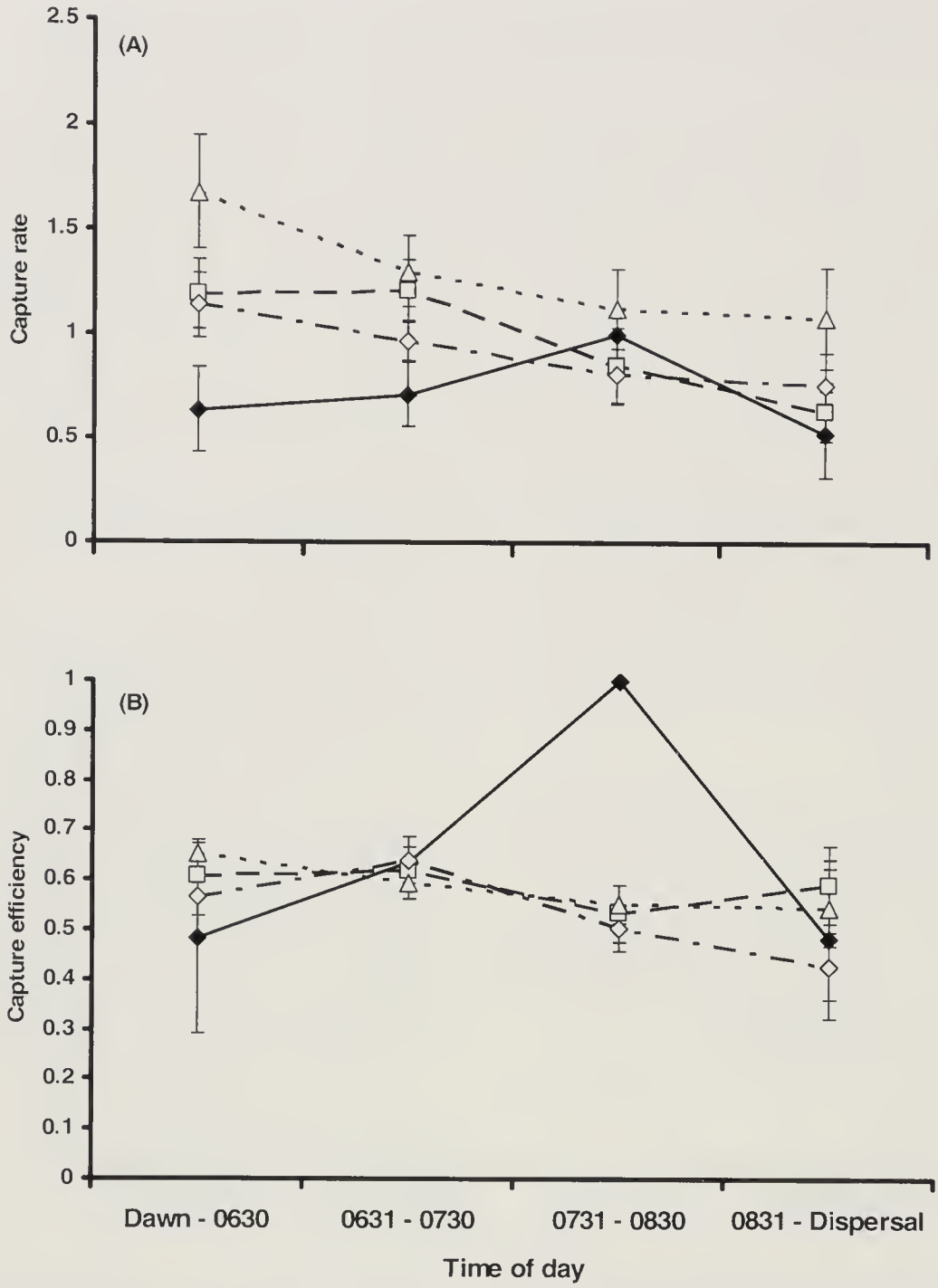

FIG. 3. Mean (± SE) (A) capture rate and (B) capture efficiency over time for Forster's Terns foraging solitarily (dark diamonds, solid line) and within aggregations of: 4 to 50 birds (open boxes, dashed line), 51 to 100 birds (open pyramids, dotted line), and >100 birds (open diamonds, variably dashed line).

probably not as many as the combined effects of multiple egrets and gulls and, thus, solitary terns dove less often for prey items, which ultimately reduced their capture rates. However, solitary birds also missed less frequently, likely due to lack of interference from waders and gulls, and their capture efficiency was similar to that of aggregated terns.

Ultimately, the tactics of Forster's Terns reflect the apparent advantages and disadvantages of aggregated versus solitary foraging over the course of the morning. Terns flew over the salt marsh, encountering multiple pools that either were or were not occupied by an aggregation. Terns could easily join a group or forage alone,. or switch between the two tactics. Incentives for joining a group were high as long as the aggregation was not so large that competition was high and prey items had been depleted, conditions that seemed to exist during the early morning. Terns foraging alone had fewer opportunities to capture prey, but they were equally likely to catch fish throughout the day as their prey had not been over-exploited and they had far less competition.

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ABUNDANCE AND DISTRIBUTION OF WATERBIRDS IN THE LLANOS OF VENEZUELA

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ABSTRACT.—The Llanos is a significant waterbird site in the Western Hemisphere, but abundance and distribution of waterbirds across this vast region are poorly known, which hampers conservation initiatives. We used point counts along road routes in the Llanos region of Venezuela to examine abundance and distribution of waterbirds during 2000–2002 within five ecoregions across the Llanos. We detected 69 species of waterbirds and recorded 283,566 individuals, of which 10 species accounted for 80% of our observations. Wading birds (Ciconiiformes) represented the largest guild both in numbers of species (26) and individuals (55%), followed by waterfowl (26%), and shorebirds (11%). Five species comprised 62% of all individuals: Cattle Egret (*Bubulcus ibis*), White-faced Whistling Duck (*Dendrocygna viduata*), Black-bellied Whistling Duck (*D. autumnalis*), Great Egret (*Ardea alba*), and Wattled Jacana (*Jacana jacana*). Wading birds were particularly ubiquitous with at least 21 of 26 species recorded in each of the ecoregions. Species richness (66), proportion of waterbirds detected (54%), and mean number of birds per route (1,459) were highest in the Banco-Bajio-Estero savanna ecoregion. Our study provides the most comprehensive data set available on waterbirds in the Llanos of Venezuela and highlights regions of special conservation concern. *Received 20 April 2009. Accepted 7 October 2009.*

The Llanos is the second largest savanna ecosystem in South America after the Cerrado of Brazil, covering some 451,474 km^2 of which two-thirds occur in Venezuela and the remainder in Colombia (Bibby et al. 1992, Mittermeier et al. 1998). Wetlands in the Llanos are concentrated in southwest Venezuela and eastern Colombia and can cover an estimated 107,530 km^2, which makes the Llanos the second largest wetland complex in South America after the Brazilian Pantanal (Hamilton et al. 2002).

This vast expanse of wetlands, along with poor soils for agriculture and low human population density, combine to make the Llanos one of the most significant waterbird habitats in the world (Scott and Carbonell 1986, Roca et al. 1997, Mittermeier et al. 1998). Over 80 species of waterbirds have been recorded in Llanos wetlands, of which the major groups are wading birds, sandpipers and plovers, waterfowl, and rails (Hilty 2003). Waterbird occurrence in the Llanos has been documented and general range maps are available in field guides (Hilty 2003), but detailed information on abundance and distribution is lacking and often dated, sparse, or limited in scope and duration (e.g., Ramo and Busto 1984, Frederick and Bildstein 1992, Tamisier and Dehorter 2000).

Little is known about abundance and distribution patterns of waterbirds in the Llanos despite its huge size and significance as waterbird habitat (Hilty 2003). This lack of information is noteworthy because the Llanos, after many years of relative isolation, is experiencing increased human population growth and accompanying disturbance including road construction, water control activities, and hunting, all of which can affect waterbird populations (Bisbal 1988, Mittermeier et al. 1998). Lack of information on waterbird populations in the Llanos seriously hampers informed conservation decisions. Our objective was to conduct a geographically extensive survey to examine the abundance and distribution of waterbirds across this vast wetland savanna landscape.

METHODS

Study Area.—The Llanos is a vast sedimentary plain bordering the Orinoco River and its tributaries. Average annual temperature exceeds 24° C and rainfall varies from 500 to 4,000 mm/year (Sarmiento 1983, Mittermeier et al. 1998, Sarmiento and Pinillos 2001). Precipitation is highly seasonal (May–Sep) with 23% of the Llanos floodplain susceptible to seasonal flooding at maximum inundation. In contrast, only 2,080 km^2 of open water remain during the dry season (Nov–Mar), principally in rivers and lakes (Hamilton et al. 2002). This interaction of seasonal rainfall, soil quality, topography, high temperatures, and fire promotes savanna vegetation across much of the Llanos, regardless of seasonal inundation. Moist gallery forest, dry tropical forest, permanent

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wetlands, and agriculture occur throughout the Llanos and contribute to a complex mosaic of habitats across the landscape (Sarmiento 1983, Huber and Alarcón 1988).

Vegetation and Ecoregions.—Several studies have delimited Llanos ecoregions based on vegetation, flooding, and soil type, but these have not produced universally accepted definitions or boundaries (Blydenstein 1967, Ramia 1967, Sarmiento 1983, Velasco and Ayarzaguena 1985, Huber and Alarcón 1988, Bulla et al. 1990). We reviewed the existing classifications and selected three well-recognized ecoregions containing most of the waterbird biodiversity in the Llanos: Alluvial Overflow Plains, Western Llanos, and Central Llanos.

The Alluvial Overflow Plains include 7.45 million ha of flat savanna grassland with gallery forest along permanent rivers (Ramia 1967, Velasco and Ayarzaguena 1985). The region is subdivided into two areas based on topography and vegetation: (1) Paspalum Savanna, and (2) Banco-Bajio-Estero Savanna (Ramia 1967, Bulla et al. 1990). Paspalum Savanna occurs in low terrain subject to extensive flooding by rivers and is dominated by *Paspalum fasciculatum*. Banco-Bajio-Estero Savanna (hereafter, BBE) borders Paspalum Savanna (hereafter, Paspalum), but topographical variations of 1–2 m create consistent differences in inundation patterns. This savanna is recognized as "banco-bajio-estero"; literally bank, slope, and marsh. Esteros are the lowest areas, bancos are higher areas of former riverbanks, and bajios are intermediate sites. Esteros comprise ~80% of the region (Sarmiento 1983, Bulla et al. 1990). The BBE includes an area of about 1 million ha of man-made impoundments (módulos). These impoundments increase maximum flood level of the savannas an average of 50 cm and prolong inundation by nearly 3 months (Bulla et al. 1990).

The Western Llanos ecoregion (5.15 million ha) is characterized by fertile soils and partial flooding (Huber and Alarcón 1988, Ramo and Busto 1988). Historically this region was deciduous tropical forest interspersed by savanna; the remaining forest fragments are now largely in reserves (Veillon 1976). Irrigation has allowed this area to become the largest rice-producing region in Venezuela (Ministerio de Agricultura y Cría 1998). We divided our sampling in this ecoregion into (1) Ricefields and (2) Western Llanos.

The Central Llanos ecoregion (7.15 million ha) consists of rolling grasslands dominated by *Trachypogon* spp. This ecoregion includes areas of chaparral dominated by the tree species *Curatella americana*, *Bowdichia virgilioides*, and *Byrsonima crassifolia*. Gallery forest, Moriche palm (*Mauritia flexuosa*) swamps, and patches of the Orinoco palm (*Copernicia tectorum*) occur where standing water persists; patches of tropical deciduous forest occurs at higher elevation (Blydenstein 1962, Ramia 1993, Huber and Alarcón 1988, Ramo and Busto 1988). Rice fields have expanded into the Central Llanos (Ministerio de Agricultura y Cría 1998).

Waterbird Surveys.—We used point counts along roadsides (Fig. 1) to survey waterbirds because roadside surveys can efficiently assess community composition and habitat associations of birds in open habitats and habitat mosaics across large landscapes (Thiollay 1978, Ellis et al. 1990, Hanowski and Niemi 1995). Detection of waterbird species in open wetlands may actually be greater from roads than off-road (Hanowski and Niemi 1995). Conway and Simon (2003) also noted that point counts along transects increase detection of less conspicuous species. Disadvantages of road count methods are recognized (Buckland et al. 2004), but we believe these limitations were not significant in our study because wetland habitats in the Llanos occur continuously along both roadsides and roadless areas.

We sampled each ecoregion based on rainfall patterns that occur in four distinct seasons, each about 3 months in duration: (1) Late Wet, July–September; (2) Early Dry, October–December; (3) Late Dry, January–March; and (4) Early Wet, April–June (Bulla et al. 1990). The hydrological extremes of these seasons were the Late Wet, which is characterized by heavy rainfall and maximum annual inundation, whereas the Late Dry is characterized by drought conditions and minimal inundation. Ecoregions were visited in the same order each season (Western, Ricefields, Central, Paspalum, and BBE), and routes were surveyed within 7 days of the calendar date surveyed each year.

An initial sample of 30 routes established in July 2000 was increased to 54 by year's end as our familiarity with the Llanos improved (Table 1). Each route was 22.5 km with 16 point-count locations spaced at 1.5-km intervals. A road was considered for route placement if at least 30 km was accessible year-round, and it was separated

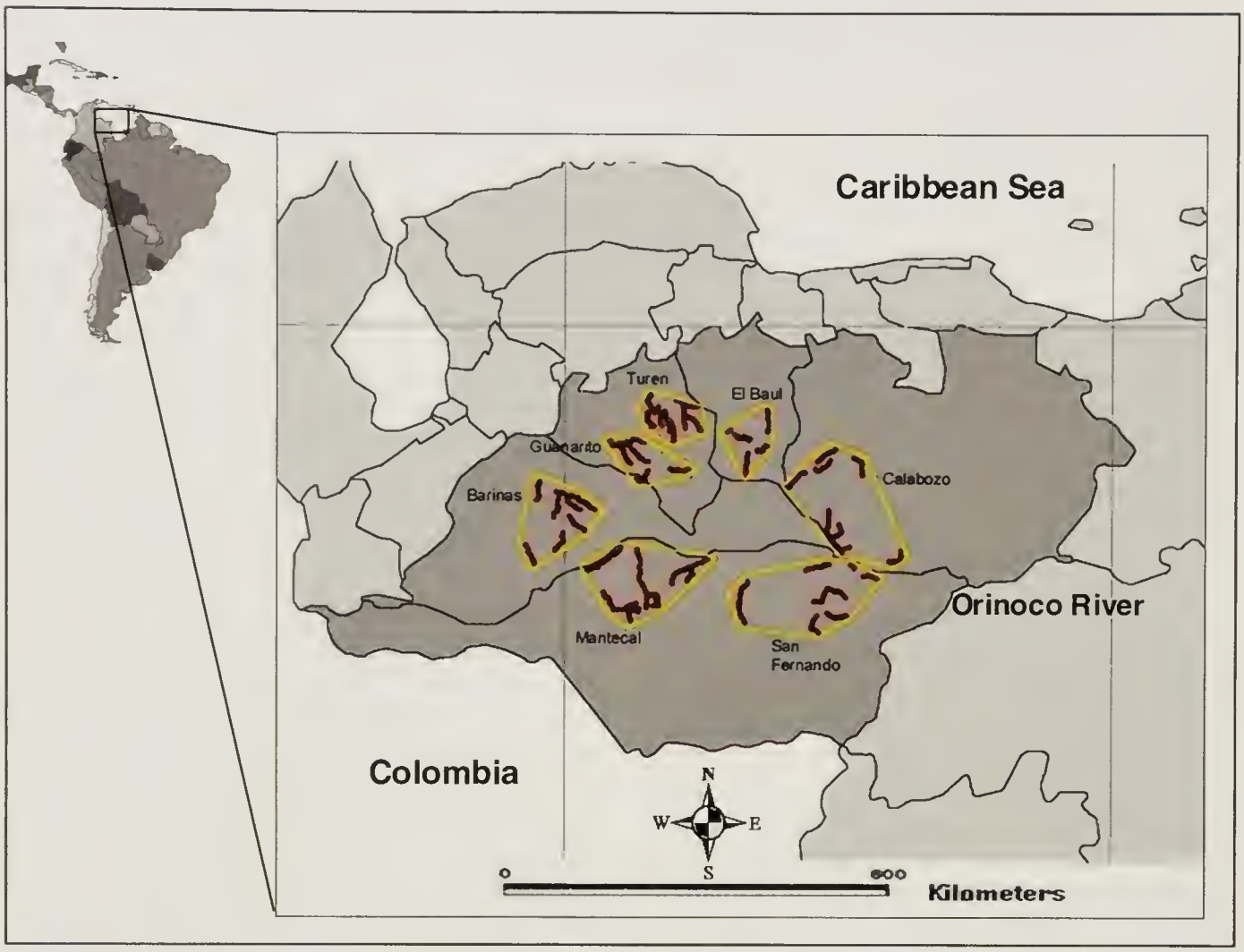

FIG. 1. Area of the Llanos of Venezuela surveyed for waterbirds. State boundaries, major cities, and route locations as referenced by GPS are included.

from another route by at least 5 km. The first point-count location was randomly selected within the first 5 km of a selected road. We used a Garmin 12 Global Positioning System (GPS) unit to identify our first point location. Road traffic was light to none and we did not believe traffic affected bird detection.

Our point count methodology was based on the North American Breeding Bird Survey (Robbins et al. 1986, Droege 1990, Peterjohn 1994) as modified by local conditions. Counts began shortly after sunrise and were usually completed by noon. A two-person team recorded all waterbirds seen or heard for 3 min within a 500-

TABLE 1. Number of routes sampled per season in each ecoregion of the Llanos, Venezuela.

		Ecoregion					
		Central	Western Llanos		Alluvial Overflow Plains		
Fieldwork periods	Season	Central	Ricefields	Western	Paspalum	BBE	Totals
14 Aug–30 Sep 2000	Late Wet	3	6	6	8	7	30
1 Nov–15 Dec 2000	Early Dry	3	6	7	10	7	33
14 Feb–31 Mar 2001	Late Dry	4	6	7	12	14	43
14 May–30 Jun 2001	Early Wet	4	8	14	14	14	54
14 Aug–30 Sep 2001	Wet	4	8	14	14	14	54
1 Nov–15 Dec 2001	Early Dry	4	8	14	14	14	54
14 Feb–31 Mar 2002	Dry	4	8	14	14	14	54
14 May–30 Jun 2002	Early Wet	4	8	14	14	14	54

m radius on each side of the road (6 min/point) as measured by rangefinder binoculars; we included birds in flight but tried to minimize double-counting. We selected the observation duration based on a January 2000 pilot study, and all observers were trained in species identification before surveys began. Observations were made using 10 × 42 binoculars and 20× spotting scopes. Common and scientific names follow Gill et al. (2009).

Data Analysis.—We selected 69 waterbird species to survey and classified these into six guilds based on feeding niche, habitat preference, and taxonomy: (1) wading birds, (2) waterfowl, (3) shorebirds, (4) open water, (5) forest, and (6) passerines. The Open Water guild comprised 13 piscivorous species requiring deep water for feeding: Least Grebe (*Tachybaptus dominicus*), Neotropic Cormorant (*Phalacrocorax brasilianus*), Anhinga (*Anhinga anhinga*), Sungrebe (*Heliornis fulica*), terns (Laridae, 4 species); and kingfishers (Alcedinidae, 5 species). The Wading Birds guild (26 species) comprised long-legged species that occur in or close to water and forage on fish, amphibians, and/or invertebrates. These included herons, egrets, and bitterns (Ardeidae, 14 species), ibises (Threskiornithidae, 8 species), storks (Ciconiidae, 3 species), and Limpkin (*Aramus guarauna*). The Waterfowl guild (10 species) included ducks (Anatidae, 8 species) and gallinules (Rallidae, 2 species). The Shorebird guild (12 species) included sandpipers (Scolopacidae, 8 species) as well as Double-striped Thick-knee (*Burhinus bistriatus*), Collared Plover (*Charadrius collaris*), Black-necked Stilt (*Himantopus mexicanus*), and Wattled Jacana (*Jacana jacana*). The Forest guild (four species) included Hoatzin (*Opisthocomus hoazin*), Grey-necked Wood Rail (*Aramides cajanea*), Sunbittern (*Eurypyga helias*), and Horned Screamer (*Anhima cornuta*). The Passerine guild included species associated with water: Pied Water Tyrant (*Fluvicola pica*), White-headed Marsh Tyrant (*Arundinicola leucocephala*), Black-capped Donacobius (*Donacobius atricapilla*), and Red-capped Cardinal (*Paroaria gularis*).

We assessed general patterns of waterbird abundance by summarizing the total numbers of birds recorded by species and guild, ranking each in order of abundance, and calculating percent relative abundance for each species. We also expressed abundance as the percentage of routes and points where we detected each species. We standardized for sampling effort in each ecoregion by calculating the mean number of each species per route per field season. We averaged mean values per sample period to derive a grand mean per route for each species or guild in each ecoregion. We used a species accumulation curve to evaluate the relationship between sampling effort and species detection over the survey period (Colwell 2006).

TABLE 2. Number of species and total number of birds recorded for each guild in the Llanos, Venezuela.

Guild	# species	% total species	Totals	% total
Wading birds	26	37.7	154,450	54.5
Waterfowl	10	14.5	74,335	26.2
Shorebirds	12	17.4	31,277	11.0
Open water	13	18.8	17,286	6.1
Forest	4	5.8	3,280	1.2
Passerines	4	5.8	2,938	1.0
Totals	69	100.0	283,566	100.0

We grouped data from both years and used *t*-tests to compare species abundance in each ecoregion and season between years; only 3.2% of the tests were significant and differences were distributed among all seasons and ecoregions. We calculated the mean number of individuals per route to combine data between years when routes were sampled in both fieldwork periods, and retained those routes added in the second period or near the end of the first. This combination standardized sample effort in each ecoregion. We compared seasonal differences in number of birds by guild in each ecoregion using analysis of variance. We used SPSS 11.0.0 for all statistical analysis, and accepted significance at the 0.05 level (SPSS 2001).

RESULTS

General Patterns.—We recorded 283,566 individuals from 69 species of waterbirds in 23 families (Appendix). The waterbird community was dominated by wading birds, which comprised 54.5% of the individuals and 37.7% of the species (Table 2). Waterfowl were second in number of individuals (26.2%), followed by shorebirds (11.0%). However, waterfowl only represented 14.5% of all species. The Open Water guild ranked second in number of species (18.8%) but fourth in abundance (6.1%). The Passerine and Forest guilds contained the fewest species (4) and individuals (1.0–1.2%). The species accumulation curve indicated sampling effort over the 2-year survey period was

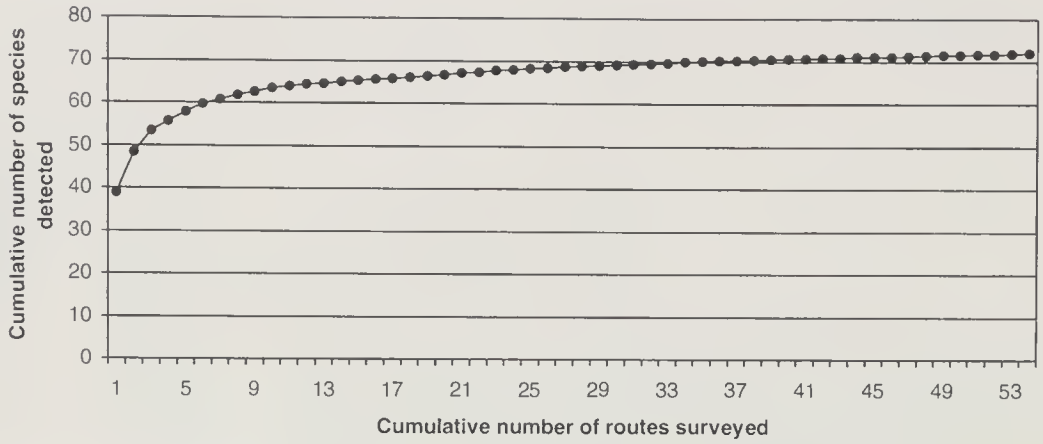

FIG. 2. Species accumulation curve for waterbird species detected during 2000–2002 surveys in the Llanos of Venezuela.

adequate for detecting most species in the study area (Fig. 2). Approximately 10 additional routes, surveyed seasonally for 2 years, would be needed to detect one additional species.

Waterbird abundance in the Llanos was dominated by a small number of species; most species occurred infrequently. Only five species comprised 62% of all individuals recorded: Cattle Egret (*Bubulcus ibis*), White-faced Whistling Duck (*Dendrocygna viduata*), Black-bellied Whistling Duck (*D. autumnalis*), Great Egret (*Ardea alba*), and Wattled Jacana. Ten species comprised 80% of all individuals recorded, and 17 species comprised 90%. The Cattle Egret was the most abundant species (23.7%) and was at 97.5% of transect sample points. The second most abundant species was the White-faced Whistling Duck (14.7%), followed by the Black-bellied Whistling Duck (10.1%). The three most abundant species collectively accounted for 48.5% of all detections. Great Egret (8.0%) and Wattled Jacana (5.9%) were much less common. We recorded <50 individuals for 14 of the 69 species detected (20.3%), including four species represented by a single observation: Sungrebe, Green-and-rufous Kingfisher (*Chloroceryle inda*), American Pygmy Kingfisher (*C. aenea*), and Least Bittern (*Ixobrychus exilis*).

Forty-one (59%) of the 69 species occurred in every ecoregion and on >50% of routes: 20 species (29%) occurred in 3–4 ecoregions, and 8 (12%) occurred in only 1–2 ecoregions. Seventeen species occurred on 90–100% of all routes, but 15 occurred on <20% of routes. Wading birds, including the Double-striped Thick-knee, were especially ubiquitous with 17 of 26 species (65.4%) occurring on >70% of all routes.

Routes in the BBE had the greatest water cover, ranging from 15 to 19% in the Late Dry season to 54–55% in the Late Wet. The Western Llanos had the lowest water cover, ranging from 4 to 5% in the Late Dry season to 11–12% in the Late Wet (Table 3).

The BBE contained the highest proportion of sample points among ecoregions with small, excavated ponds along the roadside (préstamos, 63%), followed by Paspalum (45%), Western (24%), Central (34%), and Ricefields (7%).

Species Richness and Abundance by Ecoregion.—Most waterbirds were recorded in the BBE (54%), followed by Ricefields (17%), whereas the Central had the fewest (3%, Table 4). The mean/route provides a less biased comparison among ecoregions because it standardized our sampling effort for an uneven number of routes per ecoregion (Table 5). The BBE had the highest mean number

TABLE 3. Mean (%) water cover at each point count during each fieldwork season and in each ecoregion of the Llanos. Water coverage was estimated within 200 m of each point count. No data were collected during the Late Wet season 2001.

Ecoregion	Late Wet (2000)	Early Dry (2000)	Late Dry (2001)	Early Wet (2001)	Late Wet (2001)	Early Dry (2001)	Late Dry (2002)	Early Wet (2002)
Central	11.7	15.0	9.9	9.0		11.7	7.4	12.5
Ricefields	17.4	27.8	12.6	13.8		14.5	9.7	12.9
Western	11.1	14.0	5.4	7.8		9.4	4.0	11.8
Paspalum	46.9	44.1	11.4	22.4		21.2	10.5	25.8
BBE	54.6	44.0	14.8	29.4		30.9	18.5	54.3

TABLE 4. Number of waterbirds within guilds in each ecoregion sampled in the Llanos, Venezuela, based on all routes surveyed over two field seasons.

Guild	Central	Ricefields	Western	Paspalum	BBE	Totals
Wading birds	6,115	36,330	23,944	29,554	58,507	154,450
Waterfowl	378	755	2,280	3,574	67,348	74,335
Shorebirds	449	10,085	1,518	6,045	1,005	31,227
Open water	44	703	225	4,153	12,161	17,286
Forest	152	23	591	1,110	1,401	3,280
Passerines	211	281	536	905	1,005	2,938
Totals	7,349	48,177	29,094	45,341	153,605	283,566
Percent total	2.6	17.0	10.3	16.0	54.2	

TABLE 5. Abundance of waterbirds expressed as mean (± SE) number of individuals per route in each guild for each ecoregion. Relative percentage (Rel. %) of each mean for each guild among (Rel. %-A) and within (Rel. %-W) ecoregions and species richness are included.

Guild	Central	Ricefields	Western	Paspalum	BBE
Wading birds					
Mean ± SE	200.6 ± 29.0	617.2 ± 78.4	258.9 ± 25.8	289.8 ± 10.2	574.2 ± 50.9
Rel. %-A	10.3	31.8	13.3	14.9	29.6
Rel. %-W	82.4	76.9	82.1	65.9	39.4
Richness	23	21	25	25	26
Waterfowl					
Mean ± SE	13.6 ± 4.6	11.9 ± 3.1	24.9 ± 4.2	33.4 ± 8.5	611.0 ± 240.6
Rel. %-A	2.0	1.7	3.6	4.8	87.9
Rel. %-W	5.6	1.5	7.9	7.6	41.9
Richness	6	7	7	7	10
Shorebirds					
Mean ± SE	14.9 ± 4.6	157.7 ± 48.1	15.9 ± 1.0	57.5 ± 5.6	126.6 ± 14.9
Rel. %-A	4.0	42.3	4.3	15.4	34.0
Rel. %-W	6.1	19.6	5.0	13.1	8.7
Richness	9	9	7	10	12
Open water					
Mean ± SE	1.6 ± 0.3	11.1 ± 7.0	2.5 ± 0.1	39.2 ± 1.6	122.5 ± 13.8
Rel. %-A	0.9	6.3	1.4	22.2	69.2
Rel. %-W	0.7	1.4	0.8	8.9	8.4
Richness	5	6	10	11	12
Forest					
Mean ± SE	5.8 ± 1.6	0.4 ± 0.1	7.6 ± 1.2	10.8 ± 1.9	13.8 ± 4.7
Rel. %-A	15.1	1.0	19.8	28.2	36.0
Rel. %-W	2.4	0.1	2.4	2.5	0.9
Richness	5	6	10	11	10
Passerines					
Mean ± SE	6.8 ± 1.9	4.9 ± 0.6	5.5 ± 0.7	9.0 ± 1.2	10.5 ± 1.3
Rel. %-A	18.5	13.4	15.0	24.5	28.6
Rel. %-W	2.8	0.6	1.7	2.1	0.7
Richness	4	4	4	4	4
All guilds					
Mean ± SE	243.3	803.2	315.3	439.7	1,458.6
Richness	51	49	57	61	66

of waterbirds per route (1,459/route), and the Central contained the lowest (243/route). Wading birds were the most abundant guild per route in all ecoregions (201–617/route) except the BBE, where waterfowl were most abundant (611/route). Wading birds comprised 39–82% of the mean/route in each guild. Shorebirds were most abundant in Ricefields (158/route) and BBE (127/route) but comprised <20% of all waterbirds detected within an ecoregion. Open Water species were concentrated in the BBE (123/route) and Paspalum (39/route), but were <11/route in other ecoregions and comprised <9% of all waterbirds within a guild. Forest and Passerine species were not abundant (<14/route) or proportionally substantial (<3%) in any ecoregion.

Overall species richness was greatest in the BBE (66) and least in the Central and Ricefields (Table 5). Wading birds were well represented in all ecoregions, but only the BBE included all 26 species. The fewest wading birds (21) were recorded in Ricefields. Species richness of the Open Water, Waterfowl, and Shorebird guilds showed greater variation among ecoregions than the Wading Bird guild. For example, only six of 13 species in the Open Water guild occurred in the Central and Ricefields ecoregions.

Waterbird Guilds (Wading Birds).—We recorded 154,450 wading birds with this guild dominated by herons (14 species), followed by ibises (8), and storks (3). The herons included two (Cattle Egret, Rank 1; and Great Egret, Rank 4) of the 10 most abundant species. The herons also included 4 species ranked in the top 20: Snowy Egret (*Egretta thula*), Cocoi Heron (*Ardea cocoi*), Little Blue Heron (*E. caerulea*), and Whistling Heron (*Syrigma sibilatrix*). Three species were rarely recorded: Least Bittern, Green Heron (*Butorides virescens*), and Pinnated Bittern (*Botaurus pinnatus*). Overall, herons were widespread, as 11 species occurred on >50% of routes, 12 species occurred in all five ecoregions, and eight occurred on >40% of transect sample points.

The ibis group was also widespread and frequently encountered. Three species ranked in the top 10 by abundance: Bare-faced Ibis (*Phimosus infuscatus*, Rank 6), Glossy Ibis (*Plegadis falcinellus*, Rank 7), and Scarlet Ibis (*Eudocimus ruber*, Rank 9). Ibises occurred on 57–100% of all routes and in all ecoregions with the exception of the Sharp-tailed Ibis (*Cercibis oxycerca*), which was absent from the Ricefields.

The Wood Stork (*Mycteria americana*) was most abundant; it represented only 2.6% of the wading bird guild but 74.6% of all storks and occurred on 70% of all routes. The Wood Stork also ranked 12th in overall abundance. The Maguari Stork (*Ciconia maguari*) occurred on only 43% of routes, and the Jabiru (*Jabiru mycteria*) occurred on only 35%.

Waterbird Guilds (Waterfowl).—We grouped 10 species, including the two species of gallinules into the waterfowl guild. However, 95.1% of the 74,076 individuals recorded consisted of two species: White-faced Whistling Duck and Black-bellied Whistling Duck. Only the Purple Gallinule (*Porphyrula martinica*) and Brazilian Teal (*Amazonetta brasiliensis*) of the remaining eight species exceeded 1% of the guild total. Blue-winged Teal (*Anas discors*), the only migratory species of waterfowl to reach the Llanos from North America, were rarely recorded (196 individuals).

The waterfowl guild generally was not widely distributed. Only the whistling ducks and gallinules were recorded in all ecoregions and on >50% of routes. Four species were concentrated in only one ecoregion (the Alluvial Overflow Plains): Orinoco Goose (*Neochen jubata*), Brazilian Teal, White-faced Whistling Duck, and Black-bellied Whistling Duck.

Waterbird Guilds (Shorebirds).—The Wattled Jacana was the most abundant of the 12 shorebirds, accounting for 53.6% of the 31,277 birds recorded in the guild and ranked 5th in overall abundance; the Black-necked Stilt was the second most abundant shorebird (#12). Two species occurred on >90% of routes (Wattled Jacana and Double-striped Thick-knee), but most shorebirds were more patchily distributed (8 of 12 occurred on <50% of routes), and not abundant. The South American Snipe (*Gallinago paraguaiae*) was the least frequently encountered shorebird with only eight individuals.

Waterbird Guilds (Open Water).—We recorded 13 species (17,286 individuals) in this guild, of which the Neotropic Cormorant was the most frequently recorded species (61.1%), followed by the Large-billed Tern (*Phaetusa simplex*; 18.8%). The Ringed Kingfisher (*Megaceryle torquata*) was the most abundant kingfisher (3.7%). Swimming species (Neotropic Cormorant, Anhinga, Least Grebe, Sungrebe) were more than twice as common as terns and kingfishers combined.

Open water species were primarily recorded in the BBE (69.2%); 22.2% of all observations occurred in Paspalum. The Neotropic Cormorant

accounted for >60% of observations, but all guild species were more abundant (>75% of observations) in these two ecoregions with the exception of the Least Grebe, which was recorded on only five routes, four of which were in the Western Llanos. Five species were recorded <100 times: Sungrebe, Green-and-rufous Kingfisher, American Pygmy Kingfisher, Least Grebe, and Green Kingfisher (*Chloroceryle americana*). We only encountered one Green-and-rufous Kingfisher and one American Pygmy Kingfisher.

Waterbird Guilds (Forest).—The Hoatzin was the most abundant species in this guild, representing 94.2% of the 3,280 individuals recorded. All species were observed in at least four ecoregions, but distribution was patchy (<50% of routes) and lowest in the Ricefields ecoregion.

Waterbird Guilds (Passerines).—We recorded only 2,938 individuals for the four species in this guild, of which the Pied Water Tyrant was most abundant (46.6%). All species were widespread (>80% of routes) and occurred in all ecoregions.

Temporal Patterns Within Ecoregions.—We recorded fewer waterbirds in the first fieldwork period (101,146) than the second (182,422), but combined data by seasons because seasonal differences between fieldwork periods generally were not significant (Table 6). Overall, we recorded more species and individual birds in the Late Dry season of the second fieldwork period. The proportions of waterbirds also differed between years for the Late Wet season in the BBE ($P = 0.031$) and the Early Dry season in the Central ($P = 0.015$).

Wading birds were the most abundant guild, representing >50% of all detections in all ecoregions and all seasons, except for the BBE in the Late Dry season of the second fieldwork period. There were seasonal changes in mean/route in three ecoregions ($F = 2.84$; df = 4, 49; $P = 0.056$), primarily caused by a decrease in Cattle Egrets. Wading bird numbers in the Western ecoregion were lowest in the Late Wet season (230/route) before increasing in the Early Wet season ($F = 8.13$; df = 4, 49; $P < 0.001$).

Wading bird numbers in the BBE were highest in the Late Dry season (846/route) and lowest in the Early Wet season (383/route; $F = 3.85$; df = 4, 49; $P = 0.015$). This seasonal shift in wading bird distribution between the Western and BBE ecoregion was most obvious for five ibis species: Scarlet, American White Ibis (*Eudocimus albus*), Sharp-tailed, Glossy, and Bare-faced Ibis.

Waterfowl were most abundant in the BBE ($F = 22.01$; df = 4, 49; $P < 0.001$) where we recorded >90% of all individuals, but detections in each ecoregion showed significant seasonal patterns. For example, detections in the BBE in the Late Dry season increased to nearly 2,000/route ($F = 8.06$; df = 3, 52; $P < 0.001$), because of seasonal aggregations of White-faced Whistling Ducks and Black-bellied Whistling Ducks. Waterfowl detections were lowest ($P < 0.003$) outside the BBE in the Late Dry season and increased in the Early Wet season.

The BBE was most important for shorebird abundance ($F = 9.45$; df = 4, 49; $P < 0.001$) with counts exceeding 70/route in all seasons. However, Ricefields exceeded this average in the Late Wet season, when mean route totals were 352/route with the arrival of Nearctic migrants (mostly *Calidris* and *Tringa* species). Off-route observations of *Calidris* species exceeded 2,000 individuals, but large flocks were infrequently encountered along routes. Migrants accounted for 87% of all shorebirds recorded during the Late Wet season, but this proportion decreased to 40% in the Early Dry season, as migrants dispersed.

The seasonal dynamic of shorebird abundance in the Alluvial Overflow Plains was driven mainly by detections of the Wattled Jacana. For example, numbers of Wattled Jacanas recorded in the Ricefields accounted for <5% of all shorebirds, but increased to >70% in the Western, Paspalum, and BBE. Wattled Jacanas (>100/route) were recorded in the BBE during the dry season, although the mean number of detections for shorebirds increased to >200/route in the Late Dry season with arrival of Black-necked Stilts.

Seasonal variation in the mean count per route for Open Water birds was not significant in any ecoregion except the Ricefields ($F = 3.20$; df = 3, 28; $P = 0.039$), where numbers peaked at 41 birds/route in the Late Wet season. This difference potentially resulted from flooding of the Rio Portuguesa, which was at the southern limit of the agricultural region and sampled with a single route. Over 500 Neotropic Cormorants were attracted to these temporary conditions, which raised the mean route count for the season to almost 100/route. Excluding this point reduced the average abundance of the Open Water guild in the Ricefields to <1/route in any season. Several species within the Open Water guild exhibited distinct seasonal trends. Most notably, the Yellow-billed Tern (*Sternula superciliaris*), Gull-

TABLE 6. Waterbirds (mean/route ± SE) detected across seasons for each guild and ecoregion. Means were calculated from combined data over both fieldwork seasons. Means for each guild within ecoregions that differed across seasons ($P < 0.05$) are denoted by lower case letters (one-way ANOVA and Waller-Duncan *post-hoc* comparisons).

	Central Llanos ecoregion (n = 4)			
	Late Wet	Early Dry	Late Dry	Early Wet
Guild				
Wading birds	148.5 ± 26.9	269.5 ± 130.6	156.9 ± 54.9	227.5 ± 99.0
Waterfowl	21.6 ± 12.6^{b}	1.6 ± 0.6^{a}	2.0 ± 1.7^{a}	29.3 ± 9.8^{b}
Shorebirds	28.1 ± 7.2^{b}	9.4 ± 2.7^{a,b}	14.5 ± 5.5^{a,b}	8.0 ± 2.4^{b}
Open water	2.1 ± 0.8	1.3 ± 0.6	1.8 ± 0.7	1.0 ± 0.5
Forest	4.5 ± 4.2	5.0 ± 4.0	10.5 ± 10.3	3.3 ± 3.3
Passerines	10.3 ± 2.5^{b}	4.1 ± 1.3^{a}	3.0 ± 0.5^{a}	9.8 ± 1.7^{b}
	Ricefields ecoregion (n = 8)			
	Late Wet	Early Dry	Late Dry	Early Wet
Guild				
Wading birds	321.3 ± 110.7^{a}	858.7 ± 243.9^{b}	635.0 ± 187.6^{a,b}	653.9 ± 158.0^{a}
Waterfowl	17.8 ± 5.1^{b}	20.0 ± 7.7^{b}	0.4 ± 0.3^{a}	9.6 ± 4.8^{b}
Shorebirds	351.9 ± 239.5	147.9 ± 62.3	86.4 ± 37.5	44.7 ± 12.3
Open water	41.0 ± 38.2^{b}	2.4 ± 1.5^{a,b}	0.4 ± 0.2^{a}	0.6 ± 0.2^{a}
Forest	0.2 ± 0.2	0.3 ± 0.3	0.5 ± 0.4	0.5 ± 0.4
Passerines	6.3 ± 1.5^{b}	3.6 ± 1.0^{a}	2.6 ± 1.4^{a}	7.1 ± 1.9^{b}
	Western Llanos ecoregion (n = 14)			
	Late Wet	Early Dry	Late Dry	Early Wet
Guild				
Wading birds	230.2 ± 24.4^{b}	238.3 ± 34.5^{b}	170.6 ± 38.4^{a}	396.4 ± 41.2^{c}
Waterfowl	34.5 ± 10.6^{b}	8.7 ± 2.7^{a}	14.4 ± 10.9^{a}	41.8 ± 6.4^{b}
Shorebirds	13.2 ± 1.9^{a,b}	12.4 ± 3.3^{a}	20.5 ± 3.8^{c}	17.8 ± 3.5^{b,c}
Open water	3.1 ± 0.7	2.8 ± 0.7	1.9 ± 0.4	2.2 ± 0.5
Forest	5.1 ± 2.8	4.7 ± 2.1	13.9 ± 7.9	6.9 ± 3.2
Passerines	7.0 ± 0.9^{b}	3.5 ± 0.6^{a}	3.4 ± 0.7^{a}	8.3 ± 1.3^{b}
	Paspalum ecoregion (n = 14)			
	Late Wet	Early Dry	Late Dry	Early Wet
Guild				
Wading birds	240.5 ± 38.7	301.8 ± 58.7	332.2 ± 118.3	284.8 ± 53.5
Waterfowl	36.7 ± 13.3^{c}	14.2 ± 6.0^{b}	5.5 ± 4.6^{a}	77.0 ± 32.3^{c}
Shorebirds	41.2 ± 10.7^{a,b}	38.0 ± 11.5^{a}	76.4 ± 14.0^{c}	74.6 ± 15.0^{b,c}
Open water	36.2 ± 10.5	42.5 ± 12.2	45.4 ± 17.3	32.6 ± 10.6
Forest	4.1 ± 1.4	6.3 ± 1.9	20.8 ± 11.0	12.0 ± 4.1
Passerines	12.9 ± 1.3^{b}	4.8 ± 1.0^{a}	5.4 ± 0.9^{a}	13.0 ± 1.2^{b}
	BBE (n = 14)			
	Late Wet	Early Dry	Late Dry	Early Wet
Guild				
Wading birds	582.5 ± 149.6^{a,b}	640.4 ± 87.8^{b,c}	845.8 ± 143.6^{c}	382.6 ± 46.9^{a}
Waterfowl	165.5 ± 51.0^{c}	96.9 ± 43.4^{a}	1,958.7 ± 1,254.2^{c}	223.0 ± 42.7^{b,c}
Shorebirds	71.8 ± 13.2^{a}	133.0 ± 33.9^{a,b}	201.2 ± 52.4^{b}	100.5 ± 18.8^{a}
Open water	93.5 ± 39.7	187.9 ± 89.2	137.6 ± 69.7	71.2 ± 26.6
Forest	2.2 ± 1.2	7.8 ± 3.9	39.6 ± 21.6	5.5 ± 2.9
Passerines	15.3 ± 2.2^{b}	5.4 ± 0.9^{a}	7.3 ± 1.3^{a}	13.8 ± 1.9^{b}

billed Tern (*Gelochelidon nilotica*), and Black Skimmer (*Rynchops niger*) were dry season visitors to the BBE. Anhinga and Ringed Kingfisher also became less abundant in the Late Dry season ($P < 0.05$).

The mean per route for the Forest guild was greatest in all ecoregions at the end of the dry season, peaking at 40/route in the BBE as flocks of Hoatzin became more common. Counts during the dry season also increased for the Sunbittern but seasonal differences in abundance were not significant in any ecoregion ($P > 0.05$). Passerines were most abundant in the BBE and Paspalum ($F = 6.00$; df = 1, 4; $P < 0.001$) but seasonal abundance was similar among ecoregions. The fewest passerines were detected in all ecoregions during the Early and Late Dry seasons ($P < 0.052$).

DISCUSSION

The Llanos support a diverse and abundant community of wetland dependent birds. We emphasize three major findings: (1) the waterbird community is dominated by wading birds, (2) waterbirds are not homogeneously distributed across the Llanos ecosystem, and (3) comparatively few species comprised the majority of individuals recorded. The savanna wetlands of the Pantanal of Brazil are similarly dominated by wading birds (Figueira et al. 2006). Like the Pantanal, waterbird communities of the Llanos of Venezuela were characterized by habitat generalists. Specialization is a function of the number of habitats used (Rotenberry and Wiens 1980). The waterbirds of the Llanos, both residents as well as seasonal species, generally occurred in a variety of wetland types within and between ecoregions. This may reflect the ecological flexibility and/or similarities among these habitats regarding structure and food availability. This flexibility may reflect the spatiotemporal habitat heterogencity of the Llanos and may be fundamental to maintaining local diversity of waterbirds.

We found significant spatial and temporal heterogeneity across this vast savanna ecosystem. Specifically, 70% of all waterbirds recorded occurred in the Alluvial Overflow Plains (BBE and Paspalum); Ricefields ranked a distant second at 17%. The BBE, within the Alluvial Overflow Plains, contained the most waterbird detections per route (1,459) and was especially important during the dry seasons. The wettest ecoregion during all seasons was the Alluvial Overflow Plains averaging 11–55% water cover at each sample point during each field season. The BBE was especially wet during the dry seasons (11–44%), even exceeding water cover of the Ricefields (10–27%). Overall, 63% of all half-points sampled in the BBE and 45% in the Paspalum contained permanent water in the form of préstamos along the roadside versus 7% in Ricefields, 24% in the Western Llanos, and 34% in the Central. Many species, especially in the dry seasons, shift distributions in response to these hydrological patterns, concentrating in the Alluvial Overflow Plains. The BBE contained the highest relative percentage of each waterbird guild, while the Paspalum usually ranked second or third (Table 5).

Only a few of the 69 waterbird species dominate the abundance of waterbirds we encountered in the Llanos. Nearctic migrants had marked seasonal patterns of abundance. We recorded only 196 Blue-winged Teal during our 2-year study, despite Venezuela's recognition as an important wintering site for this species (Botero and Rusch 1988). Most migrant waterbirds travel and winter along the Caribbean coast of Venezuela with smaller numbers in the inland wetlands (Rodner 2006). Recent surveys have also highlighted the importance of the northern Orinoco Delta of Venezuela as migratory shorebird habitat (Rodner 2006). The BBE was the most important ecoregion for migrant shorebirds in the Llanos (Thomas 1987). Numbers increased in the Ricefields during the Late Wet season.

Waterfowl were mainly concentrated in the BBE and Ricefields ecoregions with decreasing detections in all other ecoregions sampled. Only Black-bellied and White-faced whistling ducks were recorded in all ecoregions. Waterfowl exhibited a distinct relationship between seasonal patterns of abundance in different ecoregions, which generally reflected the transition from the Late Dry season to the Early Wet season. Waterfowl hunting is permitted during the breeding season for some species, particularly whistling ducks, which are considered serious rice crop pests (Sanz-Agreda 1998). Our surveys recorded dramatically reduced numbers of whistling ducks in the Llanos compared to estimates reported by Gómez-Dallmeier and Cringan (1989).

CONSERVATION IMPLICATIONS

Waterbirds tended to spread across the ecoregions during wet seasons but contracted to the Alluvial Overflow Plains in dry seasons. We

believe this ecoregion should be a focus of conservation efforts, because it contains extensive water coverage during the dry season, and supports the greatest number and diversity of Llanos waterbirds. The dominant land use in the Llanos is cattle ranching, which at current levels is compatible with sustaining waterbird populations and habitats (Ríos-Uzcátegui 1994). However, cattle ranching and agriculture can require deforestation. Widespread deforestation has occurred in parts of the Western Llanos (Hamilton et al. 1976, Veillon 1976). Extensive natural grasslands are the dominant habitat in the Alluvial Overflow Plains. Major modifications to the environment, such as dams, dikes, and deforestation have not yet occurred on most of these vast plains, and the low human density over most of the area prevents other significant impacts.

Additional studies are needed on the waterbird communities in the Llanos, particularly in the Alluvial Overflow Plains where the role of impoundments as waterbird habitats should be evaluated. Information on population dynamics and species-habitat relationships will help better understand ecological factors involved in regulating waterbird community structure and population levels. Additional studies should also survey for secretive marsh birds such as rails which, although common in the Llanos, were not detected during our study.

About 250,000 ha of private property on large ranches (hatos) operate ecotourism enterprises that attract tourists from around the world (Lara 1999). These arrangements in turn provide a strong incentive to promote wildlife conservation. Comparisons of waterbird abundance and diversity between private hatos (where wildlife is protected) versus areas where hunting is likely to occur may provide an indication of the severity of hunting pressure (Pérez and Ojasti 1996) and the role of hatos in conservation of Llanos waterbirds. Long-term conservation benefits for waterbird communities on private lands of the Venezuelan Llanos will require the continuing support of government and conservation agencies as well as outreach to landowners as a major approach toward protecting the rich waterbird heritage of this region.

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APPENDIX. Data pooled from all ecoregions, sample seasons, and years for 69 waterbird species (including *Calidris* spp.) detected on point transects. Nomenclature follows Gill et al. (2009). %RA = percentage relative abundance; % routes = the percentage detection per species on transect routes (54); % points = the percentage detection per species on transect points (864); % all points = the percentage detection on all points sampled during the project (6016). Regions = number of regions where a species was detected.

Family	Species	Guild	Sum	Rank	RA %	Routes %	Points %	% all points	Region
Podicipedidae	Least Grebe (*Tachybaptus dominicus*)	Open water	16	62	0.01	9.3	0.6	0.13	3
Phalacrocoracidae	Neotropic Cormorant (*Phalacrocorax brasilianus*)	Open water	10,559	8	3.72	75.9	28.5	9.01	5
Anhingidae	Anhinga (*Anhinga anhinga*)	Open water	866	29	0.31	77.8	25.2	5.37	5
Ardeidae	Black-crowned Night Heron (*Nycticorax nycticorax*)	Wader	1,015	28	0.36	92.6	24.5	5.68	5
	Capped Heron (*Pilherodius pileatus*)	Wader	99	55	0.03	70.4	8.1	1.28	5
	Cattle Egret (*Bubulcus ibis*)	Wader	67,156	1	23.68	100.0	97.5	57.21	5
	Great Egret (*Ardea alba*)	Wader	22,741	4	8.02	100.0	90.6	55.60	5
	Green Heron (*Butorides virescens*)	Wader	8	63	0.00	13.0	0.8	0.12	5
	Least Bittern (*Ixobrychus exilis*)	Wader	1	64	0.00	1.9	0.1	13.28	1
	Little Blue Heron (*Egretta caerulea*)	Wader	3,396	15	1.20	100.0	65.2	0.02	5
	Pinnated Bittern (*Botaurus pinnatus*)	Wader	16	62	0.01	18.5	1.4	21.46	3
	Rufescent Tiger-heron (*Tigrisoma lineatum*)	Wader	1,293	25	0.46	94.4	43.3	0.23	5
	Snowy Egret (*Egretta thula*)	Wader	5,447	11	1.92	98.1	47.5	11.90	5
	Striated Heron (*Butorides striatus*)	Wader	1,410	23	0.50	98.1	50.6	12.90	5
	Whistling Heron (*Syrigma sibilatrix*)	Wader	1,710	18	0.60	100.0	59.3	14.84	5
	Cocoi Heron (*Ardea cocoi*)	Wader	3,622	14	1.28	94.4	54.4	24.67	5
	Yellow-crowned Night Heron (*Nyctanassa violacea*)	Wader	240	48	0.08	53.7	7.1	1.26	5
Threskiornithidae	Bare-faced Ibis (*Phimosus infuscatus*)	Wader	16,005	6	5.64	100.0	75.2	24.38	5
	Buff-necked Ibis (*Theristicus caudatus*)	Wader	1,534	20	0.54	57.4	24.0	7.93	5
	Glossy Ibis (*Plegadis falcinellus*)	Wader	11,240	7	3.96	88.9	35.2	8.05	5
	Green Ibis (*Mesembrinibis cayennensis*)	Wader	327	43	0.12	68.5	13.4	2.41	5
	Roseate Spoonbill (*Ajaia ajaja*)	Wader	1,463	22	0.52	79.6	24.0	5.49	5
	Scarlet Ibis (*Eudocimus ruber*)	Wader	7,778	9	2.74	94.4	48.7	11.30	5
	Sharp-tailed Ibis (*Cercibis oxycerca*)	Wader	585	35	0.21	64.8	21.8	4.67	4
	White Ibis (*Eudocimus albus*)	Wader	254	47	0.09	77.8	12.8	2.14	5
Ciconiidae	Jabiru (*Jabiru mycteria*)	Wader	520	38	0.18	35.2	11.9	2.86	4
	Maguari Stork (*Euxenura maguari*)	Wader	858	30	0.30	42.6	16.6	4.01	3
	Wood Stork (*Mycteria americana*)	Wader	4,051	13	1.43	70.4	30.8	8.91	5
Anhimidae	Horned Screamer (*Anhima cornuta*)	Forest	123	53	0.04	25.9	5.6	1.08	4
Anatidae	Black-bellied Whistling Duck (*Dendrocygna autumnalis*)	Waterfowl	28,666	3	10.11	92.6	42.2	10.47	5
	Fulvous Whistling Duck (*D. bicolor*)	Waterfowl	177	50	0.06	16.7	2.0	0.37	3
	White-faced Whistling Duck (*D. viduata*)	Waterfowl	41,790	2	14.74	87.0	37.5	12.20	5
	Unidentified Whistling Duck (*Dendrocygna* spp.)	Waterfowl	259		0.09	9.3	0.6	0.08	3
	Muscovy Duck (*Cairina moschata*)	Waterfowl	106	54	0.04	29.6	3.1	0.47	4
	Orinoco Goose (*Neochen jubata*)	Waterfowl	575	36	0.20	7.4	2.8	1.01	1

APPENDIX. Continued.

Family	Species	Guild	Sum	Rank	RA %	Routes %	Points %	% all points	Region
Rallidae	Azure Gallinule (*Porphyrio flavirostris*)	Waterfowl	492	39	0.17	59.3	21.2	0.60	5
	Grey-necked Wood Rail (*Aramides cajanea*)	Forest	48	56	0.02	35.2	3.6	4.75	5
	Purple Gallinule (*Porphyrio martinica*)	Waterfowl	1,230	27	0.43	98.1	36.6	9.18	5
Heliornithidae	Sungrebe (*Heliornis fulica*)	Open water	1	64	0.00	1.9	0.1	0.02	1
Eurypigidae	Sunbittern (*Eurypyga helias*)	Forest	19	61	0.01	18.5	1.7	0.28	4
Aramidae	Limpkin (*Aramus guarauna*)	Wader	1,681	19	0.59	98.1	49.0	14.89	5
Burhinidae	Double-striped Thick-knee (*Burhinus bistriatus*)	Shorebird	636	34	0.22	92.6	19.8	4.02	5
Charadriidae	Collared Plover (*Charadrius collaris*)	Shorebird	135	52	0.05	22.2	2.3	0.42	4
Recurvirostriidae	Black-necked Stilt (*Himantopus mexicanus*)	Shorebird	5,223	12	1.84	68.5	22.0	5.07	5
Jacanidae	Wattled Jacana (*Jacana jacana*)	Shorebird	16,751	5	5.91	98.1	70.4	44.27	5
Scolopacidae	Greater Yellowlegs (*Tringa melanoleuca*)	Shorebird	484	40	0.17	38.9	4.6	0.75	5
	Lesser Yellowlegs (*T. flavipes*)	Shorebird	1,508	21	0.53	51.9	9.7	1.61	5
	Unidentifed *Calidris* sandpiper (*Calidris* spp.)	Shorebird	5,549	10	1.96	50.0	10.9	1.80	4
	Pied Lapwing (*Hoploxypterus cayanus*)	Shorebird	547	37	0.19	38.9	8.9	2.69	3
	Solitary Sandpiper (*Tringa solitaria*)	Shorebird	320	44	0.11	70.4	13.2	2.34	5
	South American Snipe (*Gallinago paraguaiae*)	Shorebird	8	63	0.00	3.7	0.5	0.35	1
	Spotted Sandpiper (*Actitis macularia*)	Shorebird	28	60	0.01	24.1	2.3	0.10	4
	Unidentified *Tringa* (*Tringa* spp.)	Shorebird	53		0.02	20.4	1.4	0.20	5
	Upland Sandpiper (*Bartramia longicauda*)	Shorebird	35	57	0.01	1.9	0.1	0.02	1
Laridae	Black Skimmer (*Rynchops niger*)	Open water	1,232	26	0.43	37.0	7.9	1.76	3
	Gull-billed Tern (*Gelochelidon nilotica*)	Open water	264	46	0.09	3.7	0.7	0.15	2
	Large-billed Tern (*Phaetusa simplex*)	Open water	3,243	16	1.14	57.4	34.3	11.72	4
	Yellow-billed Tern (*Sterula superciliaris*)	Open water	151	51	0.05	33.3	7.1	1.16	3
Opisthocomidae	Hoatzin (*Opisthoconus hoazin*)	Forest	3,090	17	1.09	50.0	14.2	5.39	5
Alcedinidae	Amazon Kingfisher (*Chloroceryle amazona*)	Open water	276	45	0.10	74.1	17.2	3.42	5
	Green Kingfisher (*C. americana*)	Open water	31	58	0.01	27.8	2.8	0.45	4
	Green-and-rufous Kingfisher (*C. inda*)	Open water	1	64	0.00	1.9	0.1	0.02	1
	American Pygmy Kingfisher (*C. aenea*)	Open water	1	64	0.00	1.9	0.1	0.02	1
	Ringed Kingfisher (*Megaceryle torquata*)	Open water	645	33	0.23	94.4	32.3	7.05	5
Tyrannidae	Pied Water Tyrant (*Fluvicola pica*)	Passerine	1,370	24	0.48	100.0	54.5	15.79	5
	White-headed Marsh Tyrant (*Arundinicola leucocephala*)	Passerine	756	32	0.27	88.9	35.6	9.86	5
Troglodytidae	Black-capped Donacobius (*Donacobius atricapillus*)	Passerine	367	42	0.13	81.5	20.3	4.59	5
Emberizidae	Red-capped Cardinal (*Paroaria gularis*)	Passerine	445	41	0.16	88.9	23.8	4.72	5
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PHENOLOGY OF SIX MIGRATORY COASTAL BIRDS IN RELATION TO CLIMATE CHANGE

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ABSTRACT.—The migration phenology of six species of coastal birds on Mustang Island, Texas, USA was examined for a 27-year period (1978–2005). First arrival date, last date of departure, and duration of stay were quantified for three winter and three summer residents. These three variables were analyzed for changes over time and correlation with local, regional, and global temperature indices. Mean local summer temperature increased 0.03° C/year (0.74° C overall), while mean local winter temperature increased 0.10° C/year (2.76° C overall). The three winter residents had a trend for increasingly later arrival, increasingly earlier departure, and decreased duration of stay over the 27-year period. These trends reflect a shortening of the winter season for these birds and are consistent with expected responses due to warming temperatures. The three terns representing summer residents had less homogeneity in temporal trends than the three winter residents. Correlations of local temperature with arrival and departure dates, and duration of stay yielded few significant results and no overall pattern. Only Double-crested Cormorant (*Phalacrocorax auritus*; a winter resident) and Least Tern (*Sterna antillarum*; a summer resident) had significant correlations between arrival date and arrival temperature. *Received 27 March 2009. Accepted 3 September 2009.*

The Earth's climate has warmed by ~0.6° C over the last 100 years according to the Intergovernmental Panel on Climate Change (IPCC 2001). There have been two distinct periods of warming during this time; one from 1910 to 1945 and the other from 1976 continuing to the present (IPCC 2001). The rate of warming during the latter period has been approximately twice the magnitude of the first and greater than any other time during the past 1,000 years (Walther et al. 2002). Regional changes in temperature are more significant when examining ecological changes and, in some cases, these climates have exhibited greater increases than the mean global temperature over the past 30 years. The largest regional increases have been over the middle and high latitudes of the northern hemisphere (IPCC 2001). There has been a recent paradigm shift from focusing on climatic consequences of global climate change to collecting existing evidence of current alterations in the biological activity of organisms as the result of warming temperatures (Wuethrich 2000, McCarty 2001, Walther et al. 2002, Parmesan and Yohe 2003).

Climate change has altered the activities of a broad range of organisms in a variety of ways (McCarty 2001, Walther et al. 2002). Organisms worldwide are experiencing shifts in range, breeding and migration phenology, and community structure. It should be expected that organisms in the northern hemisphere will shift their ranges northward or to higher elevations with increasing temperatures to remain within their thermal preferences. Parmesan et al. (1999) reported significant range shifts consistent with regional climate change for 22 species of non-migratory European butterflies over the past century. Grabherr et al. (1994) measured significant upward shifts in elevation in nine plant species over the previous 90 years in the Austrian Alps.

Phenology, or the seasonal timing of biological events, can also be an important tool for assessing effects of climate change. An organism may shift its range and/or adjust aspects of its phenology to cope with a changing climate. Phenological changes have been observed for a wide range of species, including woody and herbaceous plants, birds, insects and other invertebrates, amphibians, and fishes (Beebee 1995, Ahas 1999, Bradley et al. 1999, Roy and Sparks 2000, Cotton 2003). A review of phenologies for 677 species by Parmesan and Yohe (2003) found the shifts in phenology were overwhelmingly in the direction expected from climate change (87% of all cases studied). Phenological events can occur throughout the year, but most studies of phenology have focused on the spring season. This is because many biologically relevant events occur in spring that are likely to indicate an imprint of climate change since it is a transitional period. Examples of biological events that occur in spring are blooming of flowers, thawing of ice on frozen

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lakes, breeding of a variety of organisms, and migrations of butterflies and birds.

Several studies have shown that arrival dates of numerous species of migratory birds to breeding or stopover areas have been advancing over the past century (Bradley et al. 1999, Cotton 2003, Jonzén et al. 2006). In addition, the advancement of arrival has been linked to recent increases in global and regional temperatures. These findings have been documented by several studies of bird migrations (Sparks 1999, Sparks et al. 2005, Gordo and Sanz 2006).

Nearly all studies of avian migration phenology have focused on passerine species, leaving other bird groups virtually unexamined. We examined migration phenologies for six bird species on the Texas coast with diverse life histories. Our objectives were to investigate the migration phenology for winter and summer residents separately by testing the following hypotheses: (1) that phenological traits have changed over the past 27 years, and (2) that phenological traits are not independent of local, regional, and global temperature indices.

METHODS

Survey Methods.—Surveys (BEACHobs) of Mustang Island, Texas, USA began on 14 April 1978 and continue to the present. Surveys were conducted along a 11.7-km stretch of barrier island shoreline between beach Access Road 1 (27° 47.6′ N, 97° 05.1′ W) and Access Road 2 (27° 42.2′ N, 97° 09.0′ W), south of Port Aransas, Texas (Fig. 1). The primary objective of BEACHobs was to census bird species that use the beach. Other data recorded on the surveys included numbers of people, dogs, and motor vehicles, as well as atmospheric and oceanographic parameters, beach and dune morphology, tidal stage, and occurrence of natural and anthropogenic debris.

The survey protocol was established from results of several tests conducted during initial development of the survey to optimize surveying techniques with respect to direction of travel, survey frequency, and diurnal distribution of birds. The survey was then designed and conducted every other day, starting at sunrise (0600 to 0740 hrs CST) traveling from north to south. This sampling frequency ensured that bird presence was consistently represented in the data set. All surveys were conducted by one of us (AFA) from a four-wheel-drive vehicle while driving slowly southward between the two access roads. The surveyor, who was also the driver, had a clear view of birds, the great majority of which were feeding, roosting, or loafing. Vehicular traffic is permitted along many Texas barrier island beaches, and the beach is considered a roadway where all traffic laws pertain. This made conducting the survey possible.

Surveys were done under all weather conditions and took from 40 min to more than 3 hrs to complete, depending on beach conditions, abundance and diversity of bird species, and number of people. The full survey distance was not completed on rare occasions due to dangerous weather events, high storm tides, or unsafe beach surfaces. There were some gaps in the survey especially in the winter months of some years when the surveyor was unavailable (Table 1).

Most birds were seen in the swash zone (averaging 15 m wide) between the shoreline and the most recent high tide line. Birds in flight were also counted and occasionally there were small roosts of shorebirds between the high tide line and the foredune, which were also counted. Birds were usually counted individually, but block counting was used when abundance was high.

Statistical Analyses.—Data for complete calendar years from 1979 through 2004 were analyzed for the current study. Partial year data for 1978 and 2005 were used for applicable species. Statistical analyses were computed using SYSTAT 11.0 (SYSTAT Software Inc. 2004). Migration phenologies of six species (three winter and three summer residents) were examined. These six species were selected because they exhibited a clear annual pattern of occurrence (all were present one part of the year but completely absent for the other part). This allowed identification of date of arrival and date of departure for each species each year. The three winter residents were Double-crested Cormorant (*Phalacrocorax auritus*), Eared Grebe (*Podiceps nigricollis*), and Herring Gull (*Larus argentatus*). The three summer residents were Gull-billed Tern (*Sterna nilotica*), Least Tern (*S. antillarum*), and Sandwich Tern (*S. sandvicensis*).

Phenology was described by: first arrival date (FAD), last date of departure (LDD), and duration of stay (DUR). FAD was the first day of each year that a species was observed on Mustang Island. LDD was the day that a species was last seen each year. Duration of stay was calculated as the difference between LDD and FAD. If a significant (>1 week) gap in the

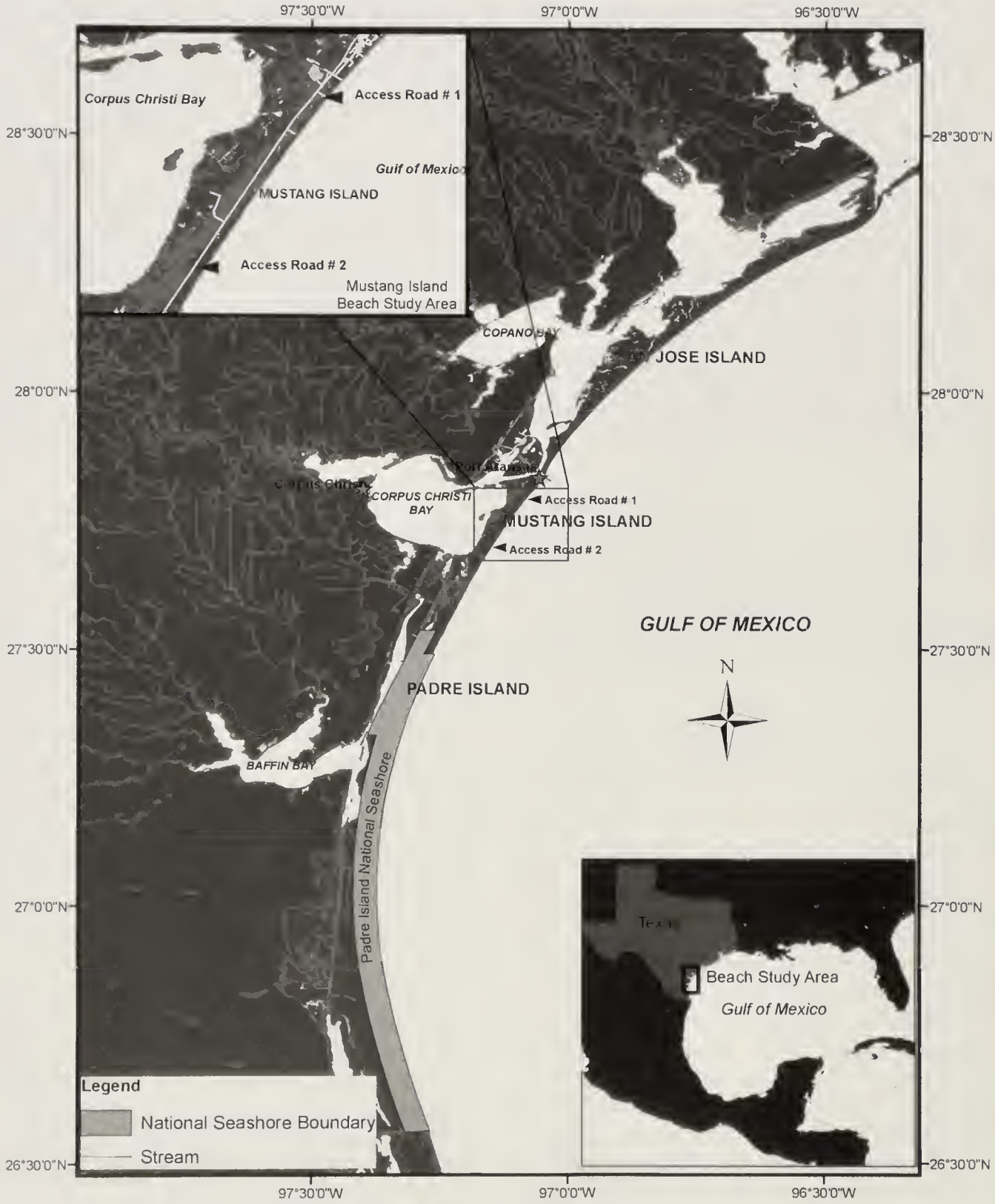


FIG. 1. Beach survey area on Mustang Island, Texas.

surveys existed during the period of arrival or departure, that year was omitted from the analysis. Temporal trends in phenological traits were described for each species using linear regression and the slope of each regression line was used to estimate the trend. The hypothesis on temporal change in a phenological trait for winter or summer residents was tested with Student's *t* statistic based on the trend value for each species (i.e., $n = 3$ trends).

Local temperature data bases were used to assess changing temperature and possible effects on avian migration phenology. These data bases included the temperature record taken during the Mustang Island beach surveys. Temperature records from Corpus Christi, Texas (~30 km

TABLE 1. Number of surveys completed by month on Mustang Island, Texas, 1978–2005.

Month	Number of surveys
Jan	208
Feb	227
Mar	323
Apr	322
May	347
Jun	320
Jul	327
Aug	335
Sep	313
Oct	303
Nov	332
Dec	266

from the survey area) were also used. These data, obtained from the NASA Goddard Institute for Space Studies (http://data.giss.nasa.gov/cgi-bin/csci/), served as an inland location less influenced by the Gulf of Mexico.

Two additional temperature data bases were used to assess the importance of large-scale climatological changes for the six species examined. Global and northern hemispheric temperature anomaly records were obtained from the Climatic Research Unit at the University of East Anglia, Norwich, UK (http://www.cru.uea.ac.uk/cru/data/temperature). These temperature records are those used by the Intergovernmental Panel on Climate Change (IPCC). The anomaly values are measures of temperature relative to the average temperature during the period of best coverage (1961–1990) and have become the standard for most studies of climate change. These global and hemispheric averages are accurate to ~+/−0.05° C (2 SEs) for the period since 1951. All four temperature indices were analyzed using linear regression to test for a significant change over time, and for correlations between temperature and migration phenology.

FAD was compared with mean temperature for the month(s) in which that particular species arrived on Mustang Island (arrival temperature). LDD was compared with the mean temperature of the month(s) during which that species left Mustang Island (departure temperature). For instance, Sandwich Terns arrived in March and departed in November or December. Arrival temperature used for the Sandwich Tern was the mean March temperature, while the departure temperature was the average of the monthly mean temperatures for November and December.

RESULTS

Local air temperature on Mustang Island, Texas increased, on average, by 0.04° C/year during 1978–2005. This overall increase of 1.08° C did not represent a significant linear trend ($P = 0.17$; Fig. 2A). However, a highly significant trend of similar magnitude (0.05° C/year) was present in the data for Corpus Christi, Texas over the same period ($P < 0.001$; Fig. 2B).

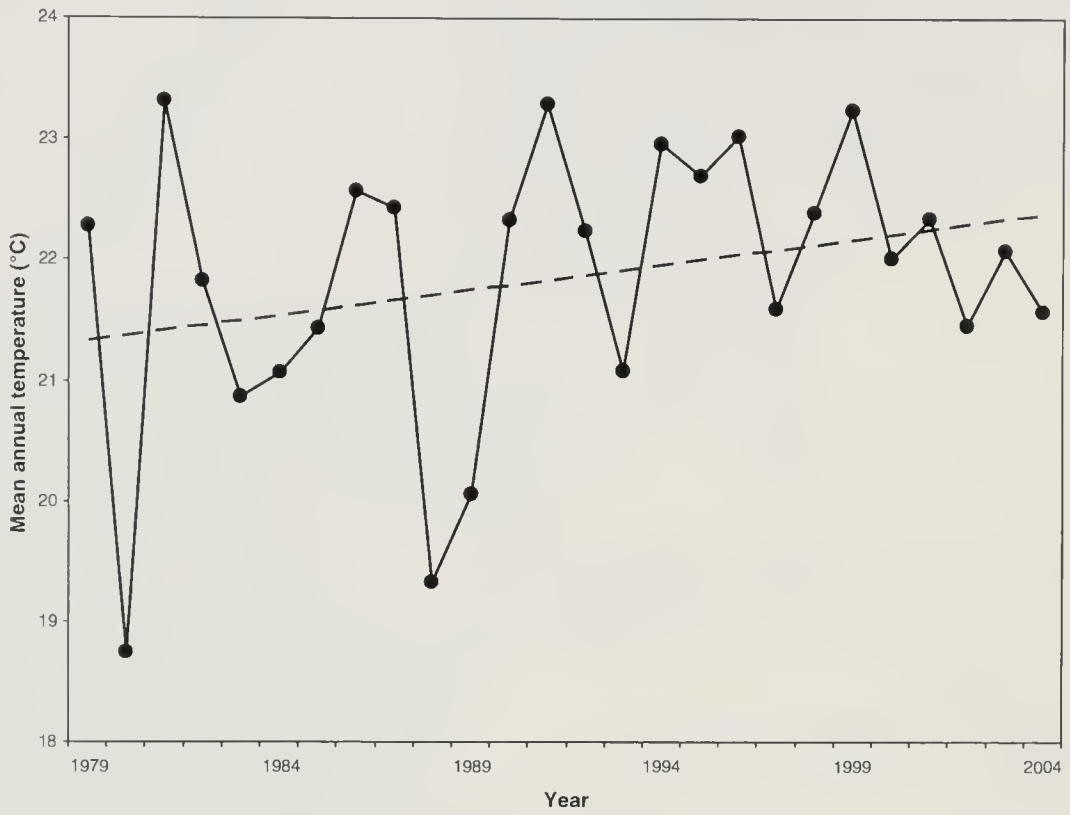
All three species that winter in the study area had positive slopes for arrival date, negative slopes for departure date, and negative slopes for duration of stay (Table 2). The mean slopes for FAD and LDD were not significantly different from zero. However, the mean slope for DUR was −0.8 days/year and demonstrated a significant departure from the null model of no change over time ($t = -5.188$, $n = 3$, $P = 0.035$; Table 2). This mean slope equates to an average decrease in duration of stay for winter residents of 21.9 days over the 27-year study period.

The three terns had less homogeneity in the temporal pattern of the phenological traits than the three winter residents. Sandwich and Gull-billed terns had a non-significant negative slope for FAD, while Least Terns had an opposite, significant trend (Table 3). All three species had negative slopes for LDD and DUR (Sandwich Tern was non-significant for both). Sandwich and Gull-billed terns had a trend toward earlier arrival, but the departure date for these two species was also earlier. The mean slope of DUR for all three species combined was not significantly different from zero ($t = -1.750$, $n = 3$, $P = 0.22$; Table 2).

Local mean winter (Dec–Feb) and summer temperatures (Jun–Aug) were calculated separately to examine the relationship between trends in phenology for winter and summer residents. Mean summer temperature increased by 0.03° C/year over 1978–2005, an overall significant increase of 0.74° C over the past 27 years ($P = 0.013$; Fig. 3). Mean winter temperature increased significantly by 0.10° C/year or 2.76° C over the same period ($P < 0.001$; Fig. 3).

Comparisons of local temperatures with arrival and departure dates, and duration of stay yielded few significant results and no consistent pattern. Only the Double-crested Cormorant, a winter resident, and Least Tern, a summer resident, had a significant correlation between arrival date and arrival temperatures and both were positive trends

(A)



(B)

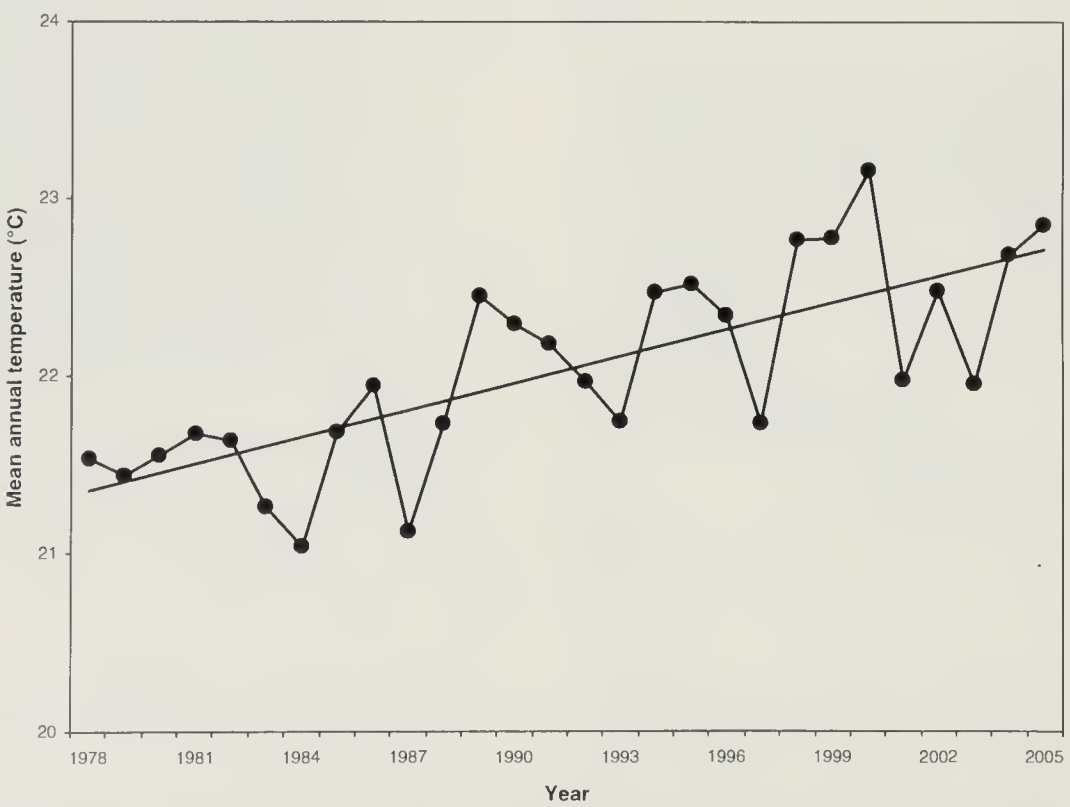


FIG. 2. Mean annual air temperature for Port Aransas, Texas (A) from 1979 to 2004 (trend not signifieant; $P = 0.17$), and for Corpus Christi, Texas (B) from 1978 to 2005 (trend is signifieant, $P < 0.001$).

TABLE 2. Slopes of regression lines and results of one-sample student's *t*-test for first arrival date (FAD), last date of departure (LDD), and duration of stay for both winter and summer species (individually significant values are in bold).

Species	Year vs. FAD	Year vs. LDD	Year vs. Duration
Winter			
Double-crested Cormorant (*Phalacrocorax auritus*)	0.409	−0.416	−0.812
Eared Grebe (*Podiceps nigricolis*)	1.262	−0.171	−0.489
Herring Gull (*Larus argentatus*)	0.141	−0.644	−0.993
Mean	0.604	−0.410	−0.765
SE	0.585	0.237	0.255
t	1.787	−3.005	−5.188
P	0.216	0.095	**0.035**
Summer			
Gull-billed Tern (*Sterna nilotica*)	−0.404	**−1.738**	−2.087
Least Tern (*S. antillarum*)	**0.462**	−0.393	**−0.825**
Sandwich Tern (*S. sandvicensis*)	−0.542	−0.436	−0.115
Mean	−0.161	−0.856	−1.009
SE	0.544	0.764	0.999
t	−0.513	−1.939	−1.750
P	0.659	0.192	0.222

(Fig. 4). The Eared Grebe, a winter resident, had a significant (negative) relationship between departure date and local departure temperature (Fig. 5). None of the six species had a significant relationship between duration of stay and local temperature. Similar results were found when temperature data from Corpus Christi, Texas were used. The temperature anomaly data sets used to represent the global and northern hemispheric temperatures over the past 27 years yielded only two significant results of a possible 36 (Gull-billed Tern and Least Tern exhibited significant relationships between DUR and global temperature) even though significant warming occurred.

DISCUSSION

The general reduction in time spent by six species of birds on Mustang Island over the past 27 years, along with confirmation that local temperatures have increased more in winter than in summer, suggests that warming temperatures may be influencing the migration phenology of three winter residents. However, when phenology variables were related directly to measures of

TABLE 3. Phenological traits for winter and summer bird species including mean ± SD, trend (slope of linear regression against year) ± SE, and *P*-value of trend (significant values in bold).

Species/residency	Arrival date				Departure date				Duration of stay			
	Mean	SD	Trend ± SE	*P*	Mean	SD	Trend ± SE	*P*	Mean	SD	Trend ± SE	*P*
Winter												
Double-crested Cormorant	07 Oct	10.970	0.409 ± 0.264	0.134	07 May	15.987	−0.416 ± 0.394	0.303	211	20.974	−0.812 ± 0.502	0.120
Eared Grebe	29 Nov	32.049	1.262 ± 0.816	0.137	19 Apr	12.809	−0.171 ± 0.358	0.638	144	28.545	−0.489 ± 0.843	0.569
Herring Gull	23 Aug	32.979	0.141 ± 0.858	0.871	28 May	16.996	−0.644 ± 0.408	0.127	278	42.647	−0.993 ± 1.090	0.372
Summer												
Gull-billed Tern	28 Mar	8.684	−0.404 ± 0.250	0.123	16 Oct	32.822	−1.738 ± 0.801	**0.040**	207	40.389	−2.087 ± 1.033	0.056
Least Tern	05 Apr	5.910	0.462 ± 0.124	**0.001**	05 Oct	11.361	−0.393 ± 0.297	0.199	183	13.575	−0.825 ± 0.320	**0.018**
Sandwich Tern	14 Mar	11.785	−0.542 ± 0.347	0.137	01 Dec	22.197	−0.436 ± 0.586	0.464	263	23.669	−0.115 ± 0.745	0.879

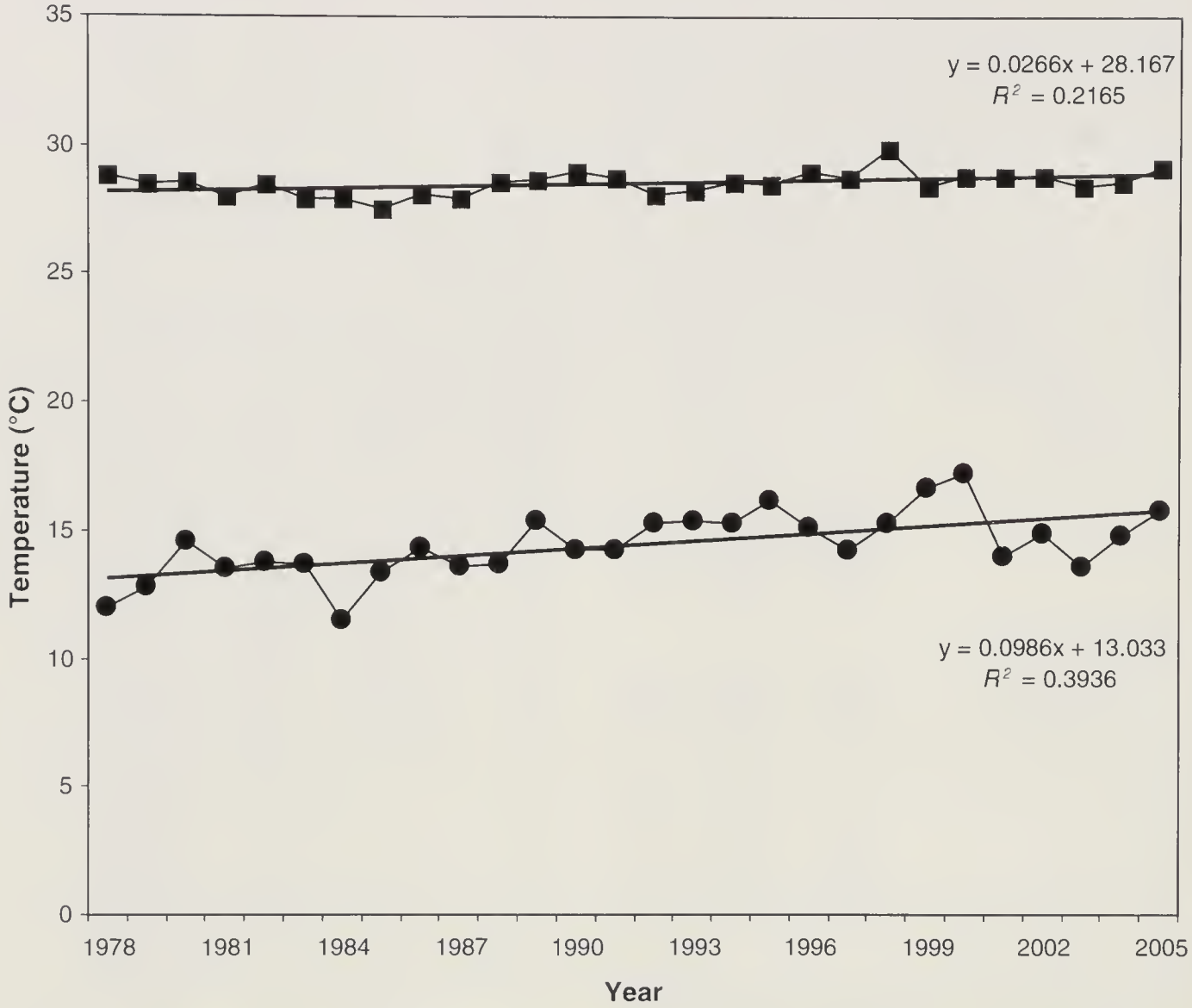


FIG. 3. Average summer (top; $P = 0.013$) and winter (bottom; $P < 0.001$) temperatures for Corpus Christi, Texas from 1978 to 2005.

local temperature, few significant correlations were found. It is possible that temperature does not have a direct effect on migration phenology at this location, but may affect other places/times along the migration route. Our results suggest that migration is triggered by conditions in breeding areas or by changes in the availability of prey items, both possible products of climate change. Double-crested Cormorants, Eared Grebes, and Herring Gulls are all widely distributed across North America. Thus, identifying whether or not climate change is affecting these birds, and where on their migration route the effects are greatest, is difficult. A lack of banding studies of these birds prohibits inferences on where the birds that winter on Mustang Island actually spend the rest of the year. However, it is known that climate change affects higher latitudes at a more rapid pace than equatorial locations (IPCC 2001). The Herring Gull has the northernmost breeding range of the three winter species examined and had the strongest trend (but not significant) toward contraction of the winter season on Mustang Island.

The three species of terns representing summer residents did not exhibit a consistent pattern in arrival date, departure date, or duration of stay. This inconsistency may arise from a smaller temperature increase during summer over the past 27 years. All three species winter from Mexico to South America. If long-term changes in phenological traits are more common in the "winter portion" of the migration cycle and temperature increase is greater in winter than in summer, terns, which winter in tropical latitudes or move to a southern hemisphere summer, might not be influenced by a long-term temperature increase. Their migratory pattern may keep them in

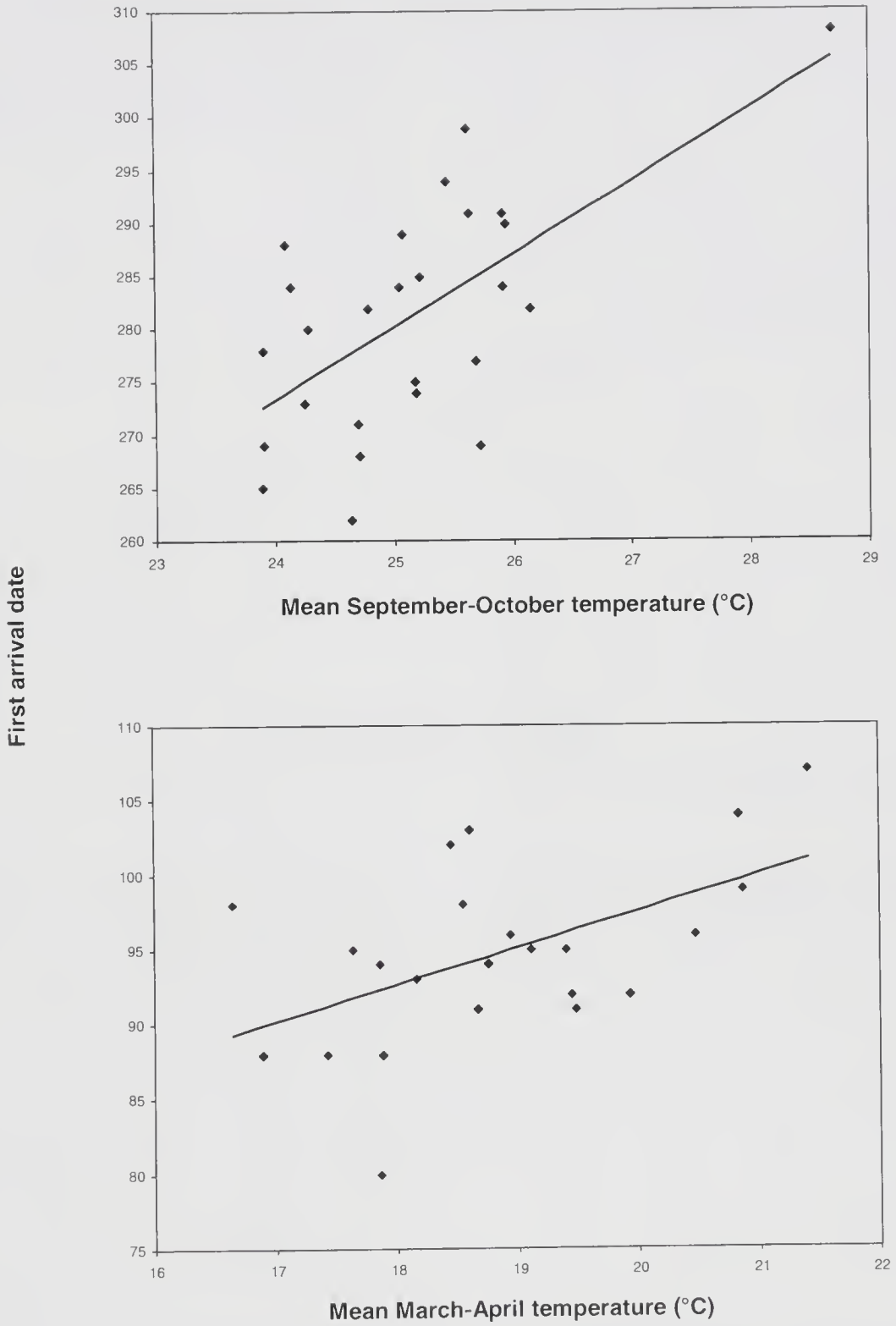


FIG. 4. Mean arrival temperature (° C) vs. first arrival date (Julian days) on Mustang Island, Texas for Double-crested Cormorant (top; $P < 0.001$) and Least Tern (bottom; $P < 0.05$) from 1978 to 2005.

"summer" temperatures year-round. All three summer residents exhibited a decrease in duration of stay on Mustang Island, although the only significant trend was for the Least Tern. Contraction of the summer season is opposite of what would be expected in a warming climate where summers should become warmer and longer. However, variability in migration phenologies has been observed in previous studies, where some species exhibit the opposite trend (Parmesan and Yohe 2003). All three terns are known to breed locally, and a decrease in amount of time on Mustang Island may translate to a shortened breeding season. Ramifications of an abridged breeding season for these species are unknown and warrant further investigation. Studies on

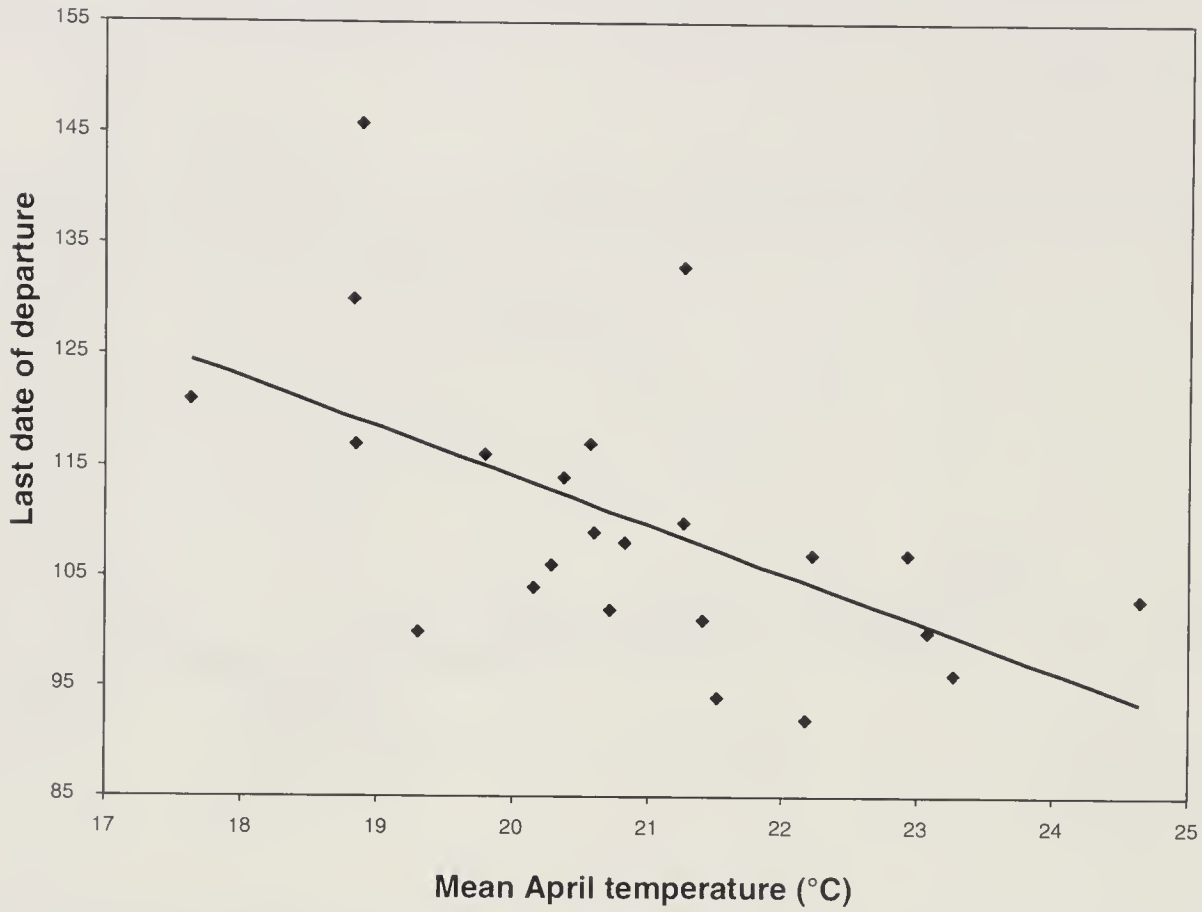


FIG. 5. Mean April (departure) temperature in Port Aransas, Texas vs. the last date of departure for Eared Grebe from Mustang Island, Texas from 1978 to 2005 ($P < 0.01$).

breeding success, clutch size, and food resources should be initiated, especially for the Least Tern which is listed as either threatened or endangered throughout its range.

A major concern in conducting phenological studies is the effect that small population size may have on the ability to detect arrival and departure dates (Sparks 1999, Tryjanowski and Sparks 2001). Conclusions on whether or not population size influences detection ability have been mixed and focused on whether a change in population size affects detection of the first arrival date. The variability in arrival and departure dates (represented by the standard deviation around the 27-year mean; Table 3) in our study was compared to the mean daily abundance of each species. Mean daily abundance among these six species ranged from 2.77 birds/day for Gull-billed Terns to 81.84 birds/day for Least Terns. No significant correlations were found between mean daily abundance and arrival date ($P = 0.28$, $n = 6$) or departure date ($P = 0.24$, $n = 6$). This suggests that, at least for this study, population size (mean daily abundance) did not cause variability in arrival and departure dates, and did not influence the ability of the observer to detect migration phenologies for these species.

Most studies of avian migration phenology have occurred in Britain (Sparks 1999, Cotton 2003) or elsewhere in Europe (Gordo and Sanz 2006, Jonzén et al. 2006) and have focused on passerine species. Information concerning breeding or migration phenology of North American birds is sparse (Brown et al. 1999, Butler 2003). Efforts are needed to assess changes in breeding and migration phenology of North American bird species to help quantify the effects of climate change. These data will allow comparisons with European studies to examine if climate change is similarly or disproportionately affecting birds on different continents. Studies of coastal birds are also needed to allow comparisons across a greater breadth of avian fauna.

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NEST-SITE LIMITATION OF SECONDARY CAVITY-NESTING BIRDS IN EVEN-AGE SOUTHERN PINE FORESTS

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ABSTRACT.—I used a randomized, replicated, controlled study design to test the hypothesis that nest-site availability limits breeding densities of secondary cavity nesting species in even-age southern pine (*Pinus* spp.) forests. Breeding densities of secondary cavity nesters increased significantly on treated plots after nest boxes were introduced. Total number of nesting attempts also increased several fold post-treatment. These data indicate nest-site availability was a limiting factor for breeding densities of secondary cavity nesting species. The response of individual species to nest boxes ranged from moderately high (Great Crested Flycatcher [*Myiarchus crinitus*]), to low (Tufted Titmouse [*Baeolophus bicolor*], Eastern Bluebird [*Sialia sialis*]) to no response (Carolina Wren [*Thryothorus ludovicianus*]). At least three factors accounted for interspecific differences in this study: different levels of reliance on cavities excavated in snags, different body sizes, and differences in local population densities. The large number of unoccupied nest boxes (only 9% were used for nesting) suggests secondary cavity nesters were not limited solely by cavity availability but also by habitat quality. Prescribed burning appeared to facilitate discovery and use of nest boxes by birds in this study, consistent with the hypothesis that nest-site limitation is mitigated by habitat structure. *Received 4 September 2007. Accepted 3 September 2009.*

Nest sites are often assumed to be the primary factor limiting densities of secondary (i.e., non-excavating) cavity-nesting birds (e.g., von Haartman 1957, 1971; Thomas et al. 1979; Cody 1985). However, tests of the nest-site limitation hypothesis by manipulative experiments, which include knowledge of initial conditions, controls, and replication (Hairston 1989), are still rare. Newton (1994) reviewed the evidence for nest-site limitation in cavity-nesting birds and found most to be circumstantial. Newton (1994) found only six studies that added or subtracted nest sites for cavity-nesting birds where controls and pre- and post-manipulation data were included. Only two of these studies (Enemar and Sjöstrand 1972, Brawn and Balda 1988) had replicate study plots. Other common biases in tests of the nest-site limitation hypothesis include lack of spatial independence of experimental and control plots (e.g., East and Perrins 1988, Beissenger and Bucher 1992), and inadequate controls because of placement of study plots in dissimilar plant communities (e.g., Brush 1983). Inadequate experimental controls can leave apparent experimental effects open to alternative explanations such as temporal and spatial variation in habitat quality.

Most nest-site limitation studies have been conducted on a small number of species inhabiting simplified European forests, especially Great Tit (*Parus major*) and European Pied Flycatcher (*Ficedula hypoleuca*), and often focusing on only one species at a time (Wesolowski 2007). Controlled nest box experiments have not been conducted with cavity-nesting birds in pine (*Pinus* spp.) forests of the southeastern United States.

Research from other forest systems indicates that cavity density is positively correlated with tree density and tree age (van Balen et al. 1982), and natural cavities formed from decay are more abundant in hardwood trees than in conifers (Waters et al. 1990). Thus, secondary cavity nesters should be more likely to be nest-site limited in younger forests and in forests dominated by conifers than in older, more structurally complex forests with abundant natural cavities (Brawn and Balda 1988, Waters et al. 1990, Wesolowski 2007).

I predicted that secondary cavity nesting species would be nest-site limited in pine forests of the southeastern United States, where silvicultural practices are considered to limit the availability of dead trees that provide nest sites for cavity nesters (McComb et al. 1986, Jackson 1988). The objective of my study was to test the hypothesis that nest-site availability limits breeding densities of secondary cavity nesting species in even-age managed pine forests, which are the predominant forest type in the southeastern coastal plain.

METHODS

Study Plots and Experimental Design.—Fieldwork was conducted on 12 study plots in 35–

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40 year-old even-age slash pine (*Pinus elliottii*) plantations at Camp Blanding Training Site, Clay County, Florida. I distributed study plots evenly between mesic "flatwoods" sites and drier "sandhill" sites to control for variation in site productivity. Flatwoods plantations were characterized by moderately to poorly drained soils and a dense shrub layer of gallberry (*Ilex glabra*), saw palmetto (*Serenoa repens*), and ericaceous shrubs (Abrahamson and Hartnett 1990). Sandhill plantations occurred on sites originally dominated by longleaf pine (*P. palustris*) (Myers 1990) and were characterized by well-drained sandy soils and a more open shrub layer. I measured live vegetation within each study plot at point-count stations (Martin et al. 1997) to develop stand profiles. Flatwoods plantations were densely stocked with a basal area ($\bar{x} \pm$ SE) of 31.0 ± 2.2 m^2/ha. Sandhill plantations were moderately stocked with a basal area of 24.5 ± 2.5 m^2/ha. All plantations had been unburned for >3 years.

I counted snags ≥10 cm diameter at breast height (dbh) on two 50 × 400 m transects within each stand. Snags were abundant (17.7 ± 2.0 [$\bar{x} \pm$ SE] snags/ha on flatwoods plots, 14.8 ± 2.1 snags/ha on sandhill plots) relative to the average of 6.2 snags/ha reported for pine plantations on public land throughout Florida (McComb et al. 1986). Most snags were too small for excavation by woodpeckers; <2% were ≥25 cm dbh (Miller 2000). More than 97.5% of all snags counted were slash pines with the remainder comprising turkey oak (*Quercus laevis*) and longleaf pine.

Study plots were of equal size (10 ha) and dimensions (250 × 400 m) and as far as possible (typically >75 m) from dirt roads and other openings. Study plots were broadly dispersed to encourage spatial independence; the northernmost study plot was 13.1 km distant from the southernmost plot, and the westernmost study plot was 9.2 km distant from the easternmost plot. Nearest-neighbor distances between study plots averaged 1.2 km (range: 0.5–2.6 km). Dense wetland forest separated the two study plots, that were only 0.5 km apart.

I applied treatments randomly in a balanced design (Table 1) after 2 years of breeding bird surveys to document initial conditions (1995–1996). Prescribed burns were conducted on two flatwoods plots and two sandhill plots during January–February 1997. Winter burns consumed leaf litter and pruned or killed shrubs and saplings, but did not cause tree mortality. I installed nest boxes during the first week of March 1997 on all burned plots and on four of the unburned plots, leaving four unburned plots without nest boxes as controls (Table 1). Two years of breeding bird surveys were conducted to assess the effects of treatments (1997–1998).

TABLE 1. Experimental design used for test of nest-site limitation. Treatments (O = no manipulation; X = nest boxes added; Y = nest boxes added after control burn) were randomly applied within forest type, Clay County, Florida, 1995–1998.

Plot #	1995	1996	1997	1998
Flatwoods				
1	O	O	O	O
2	O	O	O	O
3	O	O	X	X
4	O	O	X	X
5	O	O	Y	Y
6	O	O	Y	Y
Sandhills				
7	O	O	O	O
8	O	O	O	O
9	O	O	X	X
10	O	O	X	X
11	O	O	Y	Y
12	O	O	Y	Y

Nest Boxes.—I constructed 320 wood nest boxes with dimensions that would accommodate all species of secondary cavity nesters that breed in Florida pinelands, except raptors and waterfowl. Nest boxes differed in inside floor dimensions (10.2 × 8.9 cm or 14.0 × 14.0 cm), diameter of the entrance hole (3.5 or 5.1 cm), and in height above ground (1.9 or 4.8 m). I installed 40 nest boxes (4/ha) on each nest-box plot, at 50-m intervals in a standardized array. The nest box array was a balanced, three-factor design: box size (small vs. large) × hole size (narrow vs. wide) × box height (low vs. high). I standardized the orientation of nest boxes, placing them with the entrance hole oriented east by southeast, because cavity openings facing east, southeast, south, or southwest are typical for many cavity nesting species (Conner 1975, Pinkowski 1976, McEllin 1979, Jackson 1994, Rendell and Robertson 1994).

Nest Searches and Nest Monitoring.—I used standard methods (Martin and Geupel 1993) to search for nests in tree cavities on study plots from early April through early July 1996–1998. Each nest located was monitored regularly at 3–4 day intervals to assess nesting status (Martin

and Geupel 1993, Ralph et al. 1993). I used an aluminum extension ladder to inspect the contents of each nest box onee every 10–14 days during April–May and once every 14–21 days during June-early July 1997–1998. Nests in nest boxes also were monitored regularly at 3–4 day intervals. A nesting attempt was defined as a nest where ≥1 egg was laid.

Southern flying squirrels (*Glaucomys volans*), snakes, and other non-avian occupants were not discouraged from using nest boxes, beeause I wanted to study cavities as a limiting factor for birds under natural eonditions. Squirrel ''roost sites'' were defined as those nest boxes in which flying squirrels were observed on ≥2 occasions within a season.

Estimation of Bird Densities.—I used the intensive point count method (Ralph et al. 1993, Wilson et al. 1995) to estimate densities of breeding birds in study plots. Intensive point counts differ from extensive point counts in that points are established relatively close together within a nest search plot or mist net plot, and count data within each plot are pooled for analyses (Ralph et al. 1993). Point-count survey methods followed Ralph et al. (1993): counts were eonducted within 3 hrs post-sunrise; no counts were made during rain or strong winds; birds counted within a fixed-width circle were not recounted if they were observed moving to an adjacent fixed-width circle. I eonducted all point-eount surveys to eliminate inter-observer bias. I selected a 9-min count period because pilot studies indieated that 84% of the species in this system were detected within the first 9 min (unpubl. data); a longer count period would increase the likelihood of double counting (Seott and Ramsey 1981). Data from pilot studies demonstrated the effective detection distance was >35m for most species, including all eavity-nesting speeies. I established six 35-m radius point-count stations spaced 125 m apart within each plot (Hutto et al. 1986). Each point-count station was sampled three times per year at intervals of 2.5 weeks between 20 April and the second week of June.

Analyses of Experimental Effects.—I pooled fixed-radius point count data during each visit to a study plot because each plot was considered an experimental unit for analyses (Ralph et al. 1993). I used the maximum pooled eount for each speeies within each plot for comparisons among plots, treatments, and years. Count data were not transformed for analyses beeause of homogeneity of variances aeross treatments and years. I analyzed experimental effects with a mixed model analysis-of-variance (ANOVA) using generalized least squares estimation (PROC MIXED, SAS Institute Ine. 1997). The model ineluded four factors: treatment (control vs. nest box vs. burned with nest box), forest (flatwoods vs. sandhills), year, and a random plot effect. I modeled the differences in count data between pre- (1995, 1996) and post-treatment years (1997, 1998) using an average of the 2 pre-treatment years as a eovariate (sensitivity analysis indicated that pre-treatment years did not differ). Post-treatment years were treated separately in the ANOVA because I wanted to examine if responses to treatments changed over time. Goodness-of-fit criterion (Schwarz's Bayesian Criterion) indicated a model including interaction terms (treatment × forest, treatment × year) best described the data for each species. Pairwise differences of least-squares means (PROC MIXED) identified the relationships between variables for significant factors in the model, and P-values < 0.10 were considered significant.

RESULTS

Response of Cavity-nesting Bird Populations to Nest Box Treatments.—I detected 14 species of cavity nesters during point-count surveys. Three species of woodpeckers (Red-bellied Woodpecker [*Melanerpes carolinus*], Downy Woodpecker [*Picoides pubescens*], Northern Flicker [*Colaptes auratus*]), two species of weak excavators (Carolina Chickadee [*Poecile carolinensis*], and Brown-headed Nuthatch [*Sitta pusilla*]), and five speeies of non-excavators (Eastern Screech-Owl [*Megascops asio*], Great Crested Flyeatcher [*Myiarchus crinitus*], Tufted Titmouse [*Baeolophus bicolor*], Carolina Wren [*Thryothorus ludovicianus*], and Eastern Bluebird [*Sialia sialis*]) were documented nesting on study plots. I categorized Carolina Chickadees and Brown-headed Nuthatches as primary (i.e., excavating) cavity- nesters because of their strong affinity for cavity excavation in this locality. The other four species detected (Barred Owl [*Strix varia*], Red-headed Woodpecker [*M. erythrocephalus*], Red-eockaded Woodpecker [*P. borealis*], and Pileated Woodpecker [*Dryocopus pileatus*]) were rare (recorded on ≤1% of surveys) and did not nest on study plots.

Counts of primary cavity nesting species did not vary among treatments, either for all species

combined ($P = 0.23$) or for any individual species ($P > 0.10$). No primary cavity nester used nest boxes for nesting. Red-bellied and Downy woodpeckers accounted for 93% of all woodpeckers counted within 35-m radius point counts.

Counts of secondary cavity nesting species varied among treatments. The mixed model ANOVA for all species combined indicated that treatment was the only significant factor ($F = 7.57$, df = 2,5; $P = 0.03$) explaining the change in counts between pre-treatment (1995, 1996) and post-treatment years (1997, 1998); secondary cavity nesters increased on treated plots but decreased slightly on control plots (Fig. 1). The treatment × year interaction term approached statistical significance ($F = 2.89$, df = 2,9; $P = 0.11$), reflecting the different rates of response on unburned and burned plots. Secondary cavity nesters did not increase on unburned plots with nest boxes (NB) until 1998 but increased nearly twofold on burned plots with nest boxes (BNB) in 1997 (Fig. 1). Differences of least-squares means, post-treatment, indicated that counts ($\bar{x} \pm$ SE) were greater ($P = 0.01$) in NB plots (5.5 ± 0.7) than in control plots (2.9 ± 0.2) and greater ($P = 0.02$) in BNB plots (5.0 ± 0.4) than in control plots. Counts did not differ between NB plots and BNB plots.

Interspecific Variation in Response to Nest Box Treatments.—Treatment was the only significant factor in the mixed model ($F = 4.42$, df = 2,5; $P = 0.07$) for Great Crested Flycatchers. This species increased on treated plots after treatments were applied and decreased slightly on control plots (Fig. 2). Counts in NB plots (2.6 ± 0.4) post-treatment were greater ($P = 0.02$) than counts in control plots (1.3 ± 0.3), and counts in BNB plots (2.9 ± 0.4) were greater ($P = 0.03$) than counts in control plots. Great Crested Flycatcher numbers reached their peak during the study in the BNB plots during the first year after boxes were introduced (Fig. 2).

Tufted Titmouse response was similar to that of Great Crested Flycatchers; counts increased threefold on treated plots after treatments were applied (Fig. 2). Tufted Titmice were not recorded in fixed-radius point counts before nest boxes were introduced on any BNB plots in 1995 and on only one BNB plot in 1996 (Fig. 2). Treatment was not significant ($F = 0.37$, df = 2,5; $P = 0.70$), in part because of the small samples involved.

Eastern Bluebirds were not recorded on study plots until after nest boxes were introduced

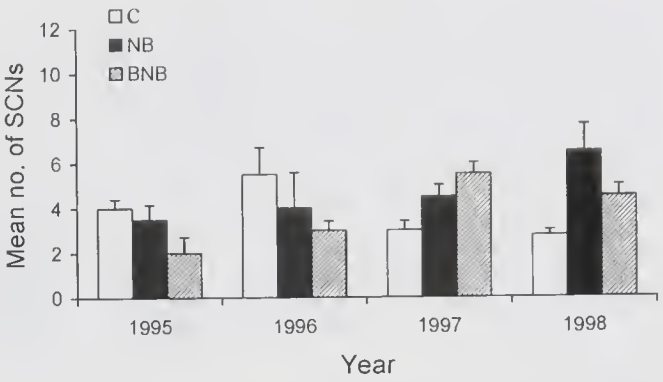

FIG. 1. Mean number of secondary cavity-nesting (SCN) birds on study plots before (1995–1996) and after (1997–1998) treatments (C = control, NB = unburned plots with nest boxes, BNB = burned plots with nest boxes). Bars equal one SE.

(Fig. 2), which suggests they responded to the nest boxes. No factors were significant, but the statistical analysis had low power because of small samples.

Carolina Wrens had no response to treatments (Fig. 2). The Carolina Wren was the only secondary cavity nester species that did not exhibit an immediate response to nest boxes in BNB plots in 1997. Forest type was the only significant factor ($F = 9.62$, df = 1,9; $P = 0.01$) explaining the differences in wren counts; wrens were more common in flatwoods plots than in sandhill plots, regardless of treatment.

Eastern Screech-Owls were not monitored effectively by point-count surveys and sample sizes were insufficient for statistical analyses.

Patterns of Nest Box Occupancy.—I recorded 57 nesting attempts in nest boxes during 1997–1998, including 33 (58%) Great Crested Flycatcher nests, 13 (23%) Tufted Titmouse nests, six (11%) Eastern Bluebird nests, three (5%) Carolina Wren nests, and two (3%) Eastern Screech-Owl nests. Screech-Owls were only able to use those nest boxes that had entrance holes enlarged by squirrels. Red-bellied Woodpeckers also were documented roosting in 19 nest boxes; these nest boxes contained fecal debris and typically were near (<50 m) an active Red-bellied Woodpecker nest in a pine snag. Overall avian occupancy of nest boxes, including woodpecker roost sites, increased from the first year (8%) to the second year (16%). Flying squirrels used 70 (22%) and 56 (18%) nest boxes as roost sites in 1997 and 1998, respectively.

The total number of secondary cavity nests on study plots increased twofold in 1997 (28 total nests) and threefold in 1998 (42 total nests)

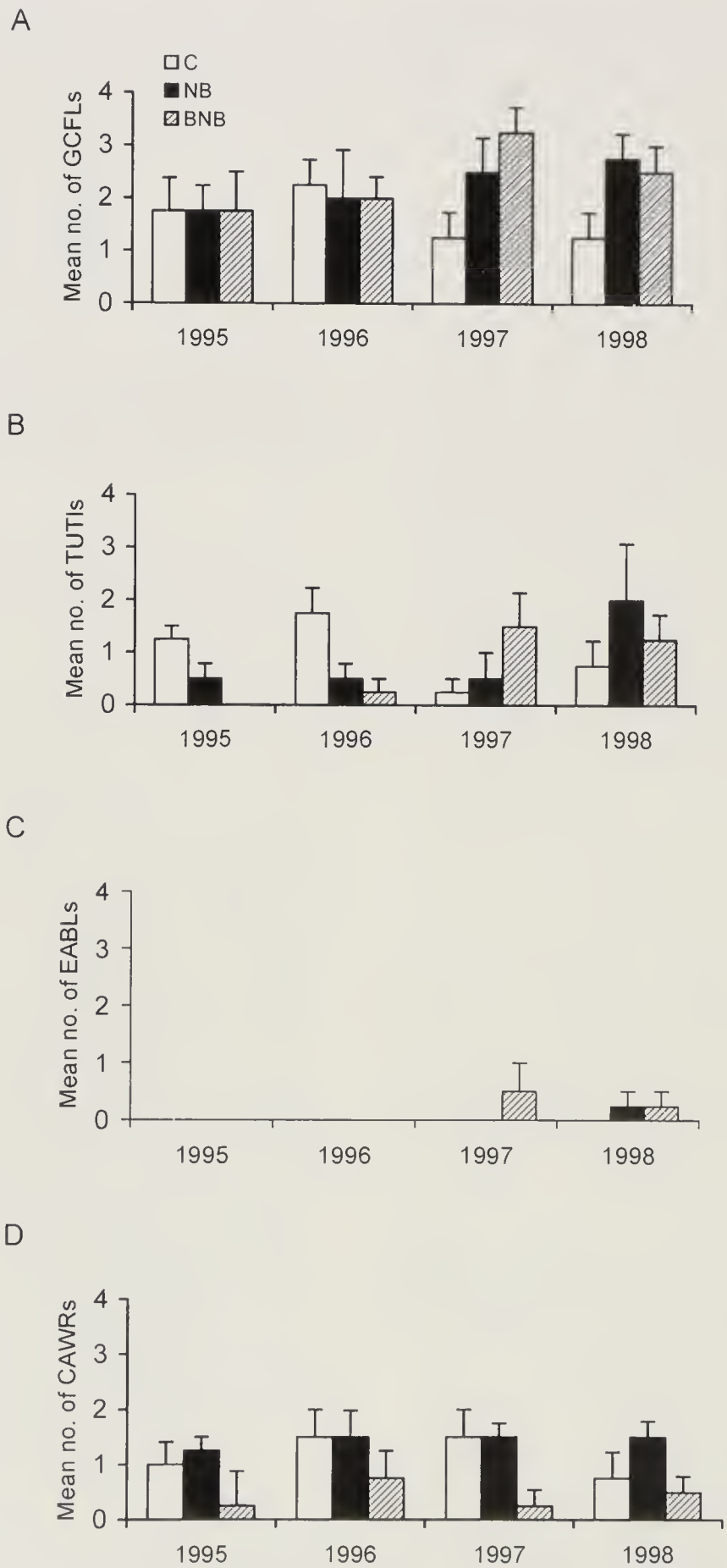

FIG. 2. Mean number of (A) Great Crested Flycatchers (GCFLs), (B) Tufted Titmice (TUTIs), (C) Eastern Bluebirds (EABLs), and (D) Carolina Wrens (CAWRs) on study plots before (1995–1996) and after (1997–1998) treatments (C = control, NB = unburned plots with nest boxes, BNB = burned plots with nest boxes). Bars equal one SE.

because of the addition of nest boxes (Table 2). Nesting activity on NB plots lagged behind that on BNB plots; cavity nesters made little use of nest boxes on NB plots until the second year after the nest boxes were in place (Table 2).

DISCUSSION

Response of Cavity-nesting Bird Populations to Nest Box Treatments.—Numbers of secondary cavity nesters recorded during the breeding season increased significantly on treated plots after nest boxes were introduced. The number of nesting attempts on treated plots also increased several fold. These data indicate that nest-site availability was limiting breeding densities of secondary cavity nesters. It is unlikely that birds moved from control to treated plots because interplot distances were many times larger than the territory sizes of these species (Grubb and Pravosudov 1994, Lanyon 1997, Gowaty and Plissner 1998). Even if a few individuals moved between plots, the slight decline in number of cavity nests on control plots (from 4 in 1996 to 3 in each of the following years; Table 2) cannot account for the large increase in the number of total nests on treated plots during 1997–1998.

Point-count surveys indicated the bird community was lacking in large-bodied woodpeckers (i.e., Northern Flicker, Pileated Woodpecker) that excavate cavities used by secondary cavity nesters. The Northern Flicker is the primary creator of large cavities used by other species in longleaf pine forest (Blanc and Walters 2008), especially larger species such as American Kestrel (*Falco sparverius*), which was absent from my study site.

TABLE 2. Nests of secondary cavity-nesting birds (Eastern Screech-Owl, Great Crested Flycatcher, Tufted Titmouse, Carolina Wren, Eastern Bluebird) in tree cavities and nest boxes, before (1996) and after (1997–1998) treatments were applied, Clay County, Florida.

	Pre-treatment		Post-treatment years			
	1996		1997		1998	
Treatment	Cavity	Box	Cavity	Box	Cavity	Box
Control plots (n = 4)	4	[a]	3	[a]	3	[a]
Nest box plots (n = 4)	6	[a]	3	5	2	16
Burned nest box plots (n = 4)	4	[a]	1	16	1	20
Totals	14	[a]	7	21	6	36

[a] Nest boxes not available.

Interspecific Variation in Nest-site Limitation.—Population response to nest boxes by individual species ranged from moderately high (Great Crested Flycatcher) to low (Tufted Titmouse, Eastern Bluebird) to no response (Carolina Wren). At least three factors accounted for interspecific differences in this study: different levels of reliance on cavities excavated in snags, different body sizes, and differences in local population densities.

Great Crested Flycatchers responded more favorably to addition of nest boxes in pine plantations than Tufted Titmice and Eastern Bluebirds, indicating they were more nest-site limited. Similarly, Ash-throated Flycatchers (*Myiarchus cinerascens*) increased from 0 to three breeding pairs after 20 nest boxes were added to a 16-ha plot of riparian forest that was devoid of cavities (Brush 1983). *Myiarchus* nest-site selection is sufficiently generalized to allow use of hollow branches and other natural cavities if they are of sufficient size (Lanyon 1997), but natural cavities available in 35–40 year-old slash pine trees apparently were too small for this species. Flycatchers relied heavily on woodpecker-excavated cavities; only one (6%) of 18 flycatcher cavity nests monitored was in a natural cavity in a living pine tree (Miller 2000).

Tufted Titmice increased in numbers following introduction of nest boxes but not as dramatically as Great Crested Flycatchers. Nest monitoring indicated that three of six (50%) titmouse nests in slash pine trees were in shallow slit cavities formed between forked pine trunks (Miller 2000). The smaller body size of the Tufted Titmouse may have allowed it to be more opportunistic in its use of natural cavities than the Great Crested Flycatcher.

Eastern Bluebirds showed only slight increases on treated plots after nest boxes were introduced. However, Eastern Bluebirds were rare on the study plots and it was difficult to assess whether they were nest-site limited. Local or regional population densities for rare species may be insufficient to provide surplus or floater individuals that would breed if more nest sites were available (Newton 1998).

Carolina Wrens had no response to treatments and, despite their abundance, rarely used nest boxes. Nest searches indicated the Carolina Wren was a facultative cavity nester at this locality, typically building its nests in crevices in brush piles, stumps, and shrubs or weaving them into

palmetto fronds (Miller 2000). Only one wren nest was found in a tree cavity during 1996–1998, a 'chimney' nest (*sensu* Wesolowski 2007) built in a low hollow stump.

Effect of Habitat on Nest-site Limitation.—The large number of unoccupied nest boxes (only 9% were used for nesting) suggests that secondary cavity nesters were not limited solely by cavity availability but also by habitat quality (e.g., unsuitable habitat structure, low food availability). Studies in western forests have demonstrated a greater response to nest boxes. For example, bird use of nest boxes in thinned ponderosa pine (*P. ponderosa*) forest in Arizona increased from 10% in the first year of their availability to 58% in the fourth year (Brawn and Balda 1988). Nest box occupancy rates in mixed oak-pine woodlands in California increased from 25% in the first year to 68% in the sixth year (Purcell et al. 1997). Extensive tree cutting during 1999–2000 curtailed my experiment, but I continued monitoring three plots unaffected by forestry operations and nest box occupancy rates during 1999–2000 did not exceed 13%. Thus, low nest box occupancy rates persisted for several years, indicating that habitat quality may set an upper limit on breeding bird density in these young forests.

Populations of several cavity nester species, especially Eastern Bluebird, were low in these densely-stocked slash pine plantations, possibly because the forest may not match the niche structure (*sensu* Grinellian niche, James et al. 1984) preferred by these species. For example, the Eastern Bluebird prefers forest gaps, forest edges, and other plant communities that have few trees and sparse ground cover (Gowaty and Plissner 1998).

Birds in flatwoods plantations and sandhill plantations responded similarly to treatments despite modest site differences in basal area and snag availability. Regardless of forest type, the response to nest boxes was most rapid on burned plots, probably because birds were attracted to areas where winter burns had opened up the shrub layer and understory. Populations of many secondary cavity nesting species respond favorably to open microhabitats created by burning (e.g., Bock and Lynch 1970, Pinkowski 1976, Hutto 1995, Kreisel and Stein 1999, Provencher et al. 2002, Allen et al. 2006).

Other Factors Potentially Limiting Cavity-nesting Bird Populations.—Breeding populations of cavity-nesting birds potentially can be limited by other factors including territoriality and interspecific competition for nest sites (Newton 1979, 1998). However, territorial behavior at present bird densities is unlikely to have prevented individuals from breeding. For example, territory mapping on study plots (unpubl. data) demonstrated that Great Crested Flycatcher territories frequently were not contiguous. The large number of nest boxes unused by birds or flying squirrels (~two-thirds of the total each year) also suggested little potential for interference competition among species. I rarely observed any evidence of inter- or intra-specific usurpation of nest boxes, although flying squirrels did depredate some flycatcher nests (Miller 2002). Interference competition for nest sites was not observed among secondary cavity nesting species at natural nests in tree cavities, although I did observe several aggressive interactions between Red-bellied Woodpeckers and Great Crested Flycatchers at Red-bellied Woodpecker nest cavities.

Nest-site limitation should not be assumed for all cavity-nesting bird species, given that some species are more opportunistic in their choice of nest sites than others. Reliance on cavities excavated in dead wood by primary cavity-nesters and larger body size were factors associated with nest-site limitation. Supporting evidence comes from studies in ponderosa pine forests, where secondary cavity nesting species that nested almost exclusively in cavities excavated by primary cavity nesters (i.e., Violet-green Swallow [*Tachycineta thalassina*]; Pygmy Nuthatch [*Sitta pygmaea*]; Western Bluebird [*Sialia mexicana*]) exhibited greater population responses to nest boxes than species that nested primarily in natural cavities and crevices (Brawn and Balda 1988).

Nest-site limitation cannot be assumed for all plant communities and locales. Tree cavities are most abundant in older forest systems, which tend to be structurally more complex (Aitken and Martin 2007, Wesolowski 2007). Results of my study provide additional support for the hypothesis that secondary cavity-nesting birds are most nest-site limited in younger forests and in forests dominated by conifers (Brawn and Balda 1988, Waters et al. 1990, Wesolowski 2007).

Prescribed burning appeared to facilitate discovery and use of nest boxes by birds in my study, which is consistent with the hypothesis that nest-site limitation is mitigated by habitat structure (Brawn and Balda 1988). If increasing cavity-nesting bird populations is a management goal in

fire-maintained habitats, such as southern pine forests, managers may find that addition of nest boxes to newly burned sites will result in the highest local densities of secondary cavity-nesting birds, at least in the short-term.

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HOUSE SPARROWS ASSOCIATED WITH REDUCED CLIFF SWALLOW NESTING SUCCESS

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ABSTRACT.—We quantified the impact of nesting and roosting House Sparrows (*Passer domesticus*) on nesting success of Cliff Swallows (*Petrochelidon pyrrhonota*) in colonies in western Arkansas in 2007 and 2008. Two sections of a large swallow colony under a bridge with House Sparrows were compared in 2007 to two sections with little House Sparrow usage. Nesting success of Cliff Swallows (percent of nests yielding at least 1 chick) was 61% in sections with low House Sparrow activity, significantly higher than the 30% in sections with high House Sparrow activity. House Sparrows defended a broad zone surrounding their nests from Cliff Swallow nesting attempts. We compared the proportion of nests used, clutch sizes, and brood sizes of Cliff Swallows in two colonies in 2008, one with and one without House Sparrow activity. In the colony without House Sparrow activity, 48% of old and new nests were used by swallows versus only 8% in the colony with House Sparrows. Swallow clutch sizes were similar in the two colonies, but swallow brood sizes in the colony with no House Sparrows were significantly higher, mean = 2.3 nestlings per nest (mode = 2; 75th percentile = 3) compared to 0.8 nestlings (mode = 0; 75th percentile = 1) in the colony with House Sparrows. This suggests Cliff Swallows are less successful when House Sparrows are present in colonies. *Received 3 April 2009. Accepted 27 September 2009.*

Cliff Swallow (*Petrochelidon pyrrhonota*) nesting colonies can contain up to 3,500 gourd-shaped mud nests adhering to rock overhangs, cliff faces, and concrete structures such as bridges and culverts (Brown and Brown 1995). Their breeding range was historically limited to mountain ranges in western North America but urbanization produced a myriad of suitable Cliff Swallow nesting sites, which allowed range expansion eastward to include most of North America. House Sparrows (*Passer domesticus*) were introduced from Europe into North America in the 1850s and 1880s (Lowther and Cink 1992). Their preference for human altered environments has enabled them to spread throughout North and Central America.

House Sparrows in North America are known to have interfered with nesting of several species of native birds (Barrows 1889, Estabrook 1907, Jackson and Tate 1974, Weisheit 1989) including Cliff Swallows (Brewster 1906, Burleigh 1930, Grinnell 1937, Stoner 1939, Bent 1942, Buss 1942, Samuel 1969, Brown and Brown 1995). Previous studies did not quantify the impact of House Sparrows on Cliff Swallow nesting effort and reproduction, or compare colonies with and without House Sparrows. Our objective was to quantify nesting effort and reproduction of Cliff Swallows in the Arkansas River valley of western Arkansas. We compared nesting of Cliff Swallows in several portions of a colony, each with different levels of House Sparrow activity, and also between two separate colonies, one with House Sparrows and one without. The three colonies were in urban or semi urban areas in or around Fort Smith, Arkansas.

METHODS

We observed an active Cliff Swallow colony in 2007 under the state highway 59 bridge spanning the Arkansas River near Barling, Arkansas in Crawford County. The bridge height made examination of nest contents impossible. Four clusters each spanning 6 m were chosen for study from over 2,100 nests: clusters A_H and B_H with high House Sparrow activity had 125 and 46 old swallow nests, clusters C_L and D_L with low House Sparrow activity had 158 and 77 old swallow nests, respectively. Subscript "L" denotes low sparrow activity while subscript "H" denotes high sparrow activity. These clusters were chosen so that A_H and C_L as well as B_H and D_L had similar density of nest aggregations, and were on opposite sides of the bridge adjacent to one another. Observations began prior to swallow nesting. Nesting in all clusters progressed similarly due to breeding synchrony of Cliff Swallows (Brown and Brown 1996).

The colony was visited twice each week. At least one cluster was observed for at least 1 hr during each visit. Extra observations were made when nestlings began to peer from nests to ensure documentation of all nests producing at least one nestling. Observations were recorded on photo-

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graphs with each nest numbered. Nest observations included identity of bird species entering nest, any nest building activity, nest defense behaviors, provisioning trips, and direct nestling observations. These data allowed quantification of nesting success of House Sparrows and Cliff Swallows in each cluster measured by proportion of available nests that yielded at least one nestling. Distance to the nearest successful Cliff Swallow nest was measured for all House Sparrow, Cliff Swallow, and European Starling (*Sturnus vulgaris*) nests. Distances between nests were measured from the center of each nest opening to the nearest 0.5 mm on photographs and scaled by measuring a known distance on each photograph.

Two colonies near Fort Smith, Sebastian County, Arkansas were studied in 2008, one with no House Sparrow activity (colony E_L; 252 old swallow nests prior to nesting) and one with high House Sparrow activity (colony F_H; 196 old swallow nests prior to nesting). Both colonies were accessible by ladder and were on the underside of highway overpasses over drainage canals. The level of House Sparrow activity at each colony was assessed prior to swallow nesting by observing their pre-roost activity, recording House Sparrows entering nests, and counting nests that were stuffed with House Sparrow nesting material.

Nest contents were observed several times throughout the nesting cycle (May–Jun) in colonies E_L and F_H using an extension ladder, dental mirror, and flashlight following Brown and Brown (1996). Nest contents were observed during the appropriate period of nesting at respective colonies to ensure documentation of eggs and nestlings. One hundred and five (41.7%) of 252 nests in colony E_L, and 118 (60.2%) of 196 nests in Colony F_H were investigated. A ladder was randomly positioned throughout the colony and all nests within reach of each ladder position were sampled. Nests were numbered with chalk on the concrete bridge substrate and monitored during visits. We recorded presence of nest material, eggshells, living and dead nestlings, and number of eggs for each nest. This information was used to quantify clutch size, brood size, and the proportion of Cliff Swallow eggs yielding successful nestlings. Active House Sparrow nests were recorded, as were clutch and brood sizes, whenever possible. Nest observations ceased before nestlings were 10 days of age to prevent premature fledging.

Chi-square contingency table analyses were performed to examine the relationship between Cliff Swallow nesting success and House Sparrow activity. Mann-Whitney *U*-tests were used to examine the difference between nesting performance (clutch size and brood size) in colonies E_L and F_H. We used SPSS (2007) in all statistical analyses.

RESULTS

House Sparrows roosting in clusters A through D gathered every evening on shrubby vegetation 3 m from the bridge for over an hour before entering their roost nests. The highest number recorded in these pre-roost congregations was 58 on 9 March 2007. Swallow nests used for roosting or nesting by sparrows were concentrated on the side of the bridge that faced nearby shrubby vegetation, which included clusters A_H and B_H.

Clusters A_H and B_H had high House Sparrow activity and were grouped together for analyses. We recorded House Sparrows entering or defending 38 nests and successfully nesting in seven nests in clusters A_H and B_H. Sparrows nesting outside our sample still defended nests within sampled clusters. These clusters also supported two European Starling nests. Cliff Swallows nested successfully (produced at least 1 nestling) in 52 of 171 available nest cavities (30.4%).

Clusters C_L and D_L were grouped together for analyses because of low House Sparrow activity. These clusters faced away from nearby shrubs. We recorded House Sparrows entering or defending eight nests and successfully nesting in only one nest. These clusters supported a single starling nest. Cliff Swallows nested successfully in 144 of 235 available nest cavities (61.3%). Cliff Swallow nesting success was significantly higher in clusters with low sparrow activity when compared to those with high sparrow activity ($\chi^2 = 37.767$, df = 1, $P < 0.001$, Table 1). Mean (± SD) distance to the nearest successful Cliff Swallow nest in clusters A–D (Table 2) was 33.2 ± 28.6 cm for nests of House

TABLE 1. Cliff Swallow (CS) nesting success (producing ≥ 1 nestling) among high or low House Sparrow activity. Data from 2007 are presented first and 2008 data are in parentheses.

	House Sparrow activity	
	High	Low
Nests containing ≥ 1 CS nestling	52 (31)	144 (41)
Empty nests	119 (112)	91 (56)

Sparrows, 16.6 ± 9.2 cm for starlings, and 11.0 ± 4.7 cm for Cliff Swallows.

Colonies E_L and F_H were observed in 2008. Colony E_L was devoid of House Sparrows except for one observation of a brief sparrow visit after most swallow eggs had hatched. An Eastern Bluebird (*Sialia sialis*) began nesting in an old Cliff Swallow nest but abandoned the nest soon after Cliff Swallows arrived on 1 April 2008. This colony had no shrubby vegetation nearby. Fifty (47.6%) of 105 sampled nests were used by Cliff Swallows for nesting. The mean (± SD) clutch size was 2.64 ± 0.12 eggs (mode = 2; 75th percentile = 3, Fig. 1) and mean brood size was 2.31 ± 0.12 nestlings (mode = 2; 75th percentile = 3, Fig. 1). At least 74% of eggs yielded nestlings in colony E_L.

Colony F_H had a high level of sparrow activity. This colony was near shrubs that House Sparrows used as pre-roosts throughout nesting. Thirty-one nests were stuffed with House Sparrow nesting material, but only 12 active House Sparrow nests were recorded. The 12 active nests produced at least 37 House Sparrow eggs. Only 10 of 118 sampled nests were active Cliff Swallow nests (8.5%). Cliff Swallows nesting in this colony (producing ≥ 1 nestling) had lower success than in colony E_L ($\chi^2 = 50.319$, df = 1, $P < 0.001$, Table 1). The mean (± SD) clutch size among Cliff Swallows in F_H was 2.60 ± 0.27 eggs (mode = 3; 75th percentile = 3, Fig. 1) but the mean brood size was only 0.83 ± 0.48 nestlings (mode = 0; 75th percentile = 1, Fig. 1). Only 20% of Cliff Swallow eggs yielded nestlings and several Cliff Swallow clutches were abandoned. Clutch size of Cliff Swallows did not differ between colonies E_L and F_H ($U = 248$, $P = 0.966$) but brood size was significantly lower in colony F_H than in colony E_L ($U = 39$, $P = 0.005$).

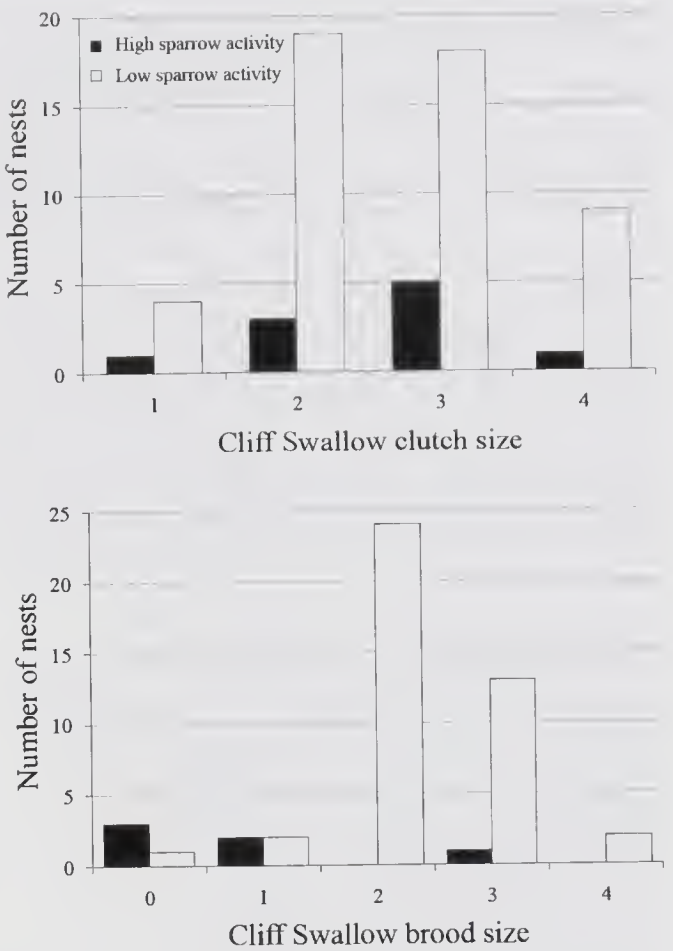

FIG. 1. Cliff Swallow clutch and brood sizes from two colonies in 2008. Colony F had high sparrow activity (black) while colony E (white) had low sparrow activity. Nests with brood size of zero are those in which eggs were documented but no nestlings were produced.

DISCUSSION

Cliff Swallow nesting success was low in both years when House Sparrows were nesting within the swallow colony. There was a 31% reduction in Cliff Swallow nests producing at least one nestling in 2007 in sections of a colony with House Sparrows, and a 54% reduction in proportion of Cliff Swallow eggs producing nestlings in 2008 in the colony with House Sparrows compared to sections without House Sparrows. House Sparrow activity was greater in nests facing and in close proximity to shrubs used as pre-roosts in all colonies.

The nesting season of House Sparrows in the southern United States begins in March (Lowther and Cink 1992), 1 month before that of Cliff Swallows (Brown and Brown 1995). House Sparrows in the present study roosted in Cliff Swallow colonies throughout winter. Our earliest observation of Cliff Swallows was 1 April 2008. House Sparrows had established themselves in old Cliff Swallow nests at this point and some were incubating eggs, similar to reports by Buss (1942) and Samuel (1969). House Sparrows defended a broad zone around their nests often preventing Cliff Swallows from nesting nearby (Table 2).

TABLE 2. Distance to the nearest Cliff Swallow (CS) nest for House Sparrows, European Starlings, and Cliff Swallows nesting in Clusters A–D in 2007.

	Mean ± SD distance (cm) to nearest CS nest	*n*
House Sparrow	33.2 ± 28.6	8
European Starling	16.6 ± 9.2	3
Cliff Swallow	11.0 ± 4.7	195

which could explain the significant impact to Cliff Swallow nesting associated with even a modest number of House Sparrows. Samuel (1969) reported that 33.6% of Cliff Swallow nests were lost to House Sparrows with most of these nests occupied before swallows began nesting, but some were taken despite Cliff Swallow eggs or nestlings being present.

House Sparrows have been observed pecking eggs and nestlings of Barn Swallows (*Hirundo rustica*) (Weisheit 1989), but the enclosed nests of Cliff Swallows made direct observation of this behavior difficult. Our data suggests this occurred in Cliff Swallow colonies as there was significantly reduced Cliff Swallow production despite similar clutch sizes in a colony with House Sparrows compared to a colony without House Sparrows. We observed a House Sparrow entering an active Cliff Swallow nest despite aggressive protest from the incubating swallow and we observed dead Cliff Swallow nestlings and unhatched eggs on the ground beneath colonies with House Sparrows; these observations are insufficient to implicate House Sparrows directly.

Buss (1942) reported successful House Sparrow management that included shooting House Sparrows and removing Cliff Swallow nests in winter to prevent sparrow roosting. We suggest that removal of nearby shrubbery could discourage House Sparrow roosting and nesting in Cliff Swallow colonies as we observed more House Sparrow activity at swallow nests facing and in close proximity to shrubby vegetation used for sparrow pre-roost congregations.

Our finding that House Sparrow activity was negatively related to the number of active Cliff Swallow nests, nesting success, brood size, and the proportion of eggs yielding nestlings indicates that House Sparrows can significantly reduce Cliff Swallow reproductive success in western Arkansas.

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HOME-RANGE SIZE AND SITE TENACITY OF OVERWINTERING LE CONTE'S SPARROWS IN A FIRE MANAGED PRAIRIE

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ABSTRACT.—We evaluated home-range size and site tenacity of Le Conte's Sparrows (*Ammodramus leconteii*) during winter 2002–2003 at Brazoria National Wildlife Refuge, Texas. Twenty-six wintering Le Conte's Sparrows were radiomarked in 1- and 2-year post-burn units, and monitored for ~10 days. Additionally, 1-ha plots on each 1-, 2- and 3-year (n = 15) post-burn units were flush-netted once monthly. Telemetry results indicated Le Conte's Sparrows were sedentary during winter with a 50% probability mean home-range of 2.41 ha (72% < 1 ha) and a 95% probability mean home range of 10.31 ha (44% < 1 ha and 55% < 1.5 ha). Home-range size did not differ between post-burn year 1 and 2 (P = 0.227). Le Conte's Sparrows appeared to exhibit a behavioral response to flush-netting (P < 0.001) with estimated capture probability of 0.462 and recapture probability of 0.056. Our findings suggest Le Conte's Sparrows remain fairly sedentary throughout the winter. *Received 28 March 2008. Accepted 7 August 2009.*

Site tenacity has been reported for many overwintering grassland birds (Plentovich et al. 1998, Gordon 2000); familiarity with an area may increase an individual's ability to acquire resources and avoid predators. Optimal management of habitats in wintering areas for high-priority species that exhibit strong site tenacity may increase overwinter survival, and enhance breeding (Pulliam and Enders 1971, Fretwell 1972, Wiens 1974, Raitt and Pimm 1976, Grzybowski 1982).

Le Conte's Sparrows (*Ammodramus leconteii*) have been listed as a "high priority species in need of conservation attention" by Partners in Flight (Carter et al. 2000, Shackelford et al. 2001). They are fairly uncommon over much of their breeding range with the highest densities in the western portions (Lowther 1996). Le Conte's Sparrows are poorly covered by the North American Breeding Bird Survey, in part due to their secretive behavior (Igl and Johnson 1999). Similarly, during the non-breeding season, the species may be underestimated or undetected on many Christmas Bird Counts. Concern for this species is compounded by severe habitat loss in wintering areas. Wintering areas, primarily coastal prairie, still used by this species and other grassland-dependent birds are degraded largely due to fire suppression, agricultural practices and, more recently, invasive plant species (Grace 1998, Igl and Ballard 1999, Allain and Grace 2001). Knowledge of Le Conte's Sparrow ecology and space use during winter can facilitate efforts to provide optimal habitat during the non-breeding season.

Little is known about the general ecology of Le Conte's Sparrow (Igl and Johnson 1999), especially during winter. They reluctantly flush from observers and spend much of their time on or near the ground in dense vegetation. Most literature related to Le Conte's Sparrow refers to their ecology and behavior during the breeding season (Madden et al. 1999, Johnson and Igl 2001, Winter et al. 2005). Few studies have examined Le Conte's Sparrow winter ecology. Igl and Ballard (1999) evaluated habitat associations of migrating and overwintering grassland birds in southern Texas. Their study showed significant differences in densities of Le Conte's Sparrows among habitats during both winter and spring but not in the fall. Baldwin et al. (2007) examined habitat relations in coastal prairie and found Le Conte's Sparrows are most common in areas burned ≤2 years and characterized by medium herbaceous density and sparse shrubs. Reynolds and Krausman (1998) examined relative abundance between unburned and recently burned (<1-year) plots in a mesquite (*Prosopis* spp.) grassland, and found Le Conte's Sparrow abandoned recently burned areas. Grzybowski (1983) measured frequency of occurrence of individuals

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to describe patterns of space use. His results suggested that Le Conte's Sparrow are solitary during winter and appear to inhabit small home-ranges, as they were only spaced 11–42 m from other individuals (Grzybowski 1983). His findings provided important information concerning space use by Le Conte's Sparrow during winter, but Grzybowski (1983) examined unmarked birds and there is uncertainty regarding individual site tenacity, and their sedentary tendencies during the winter. Lorenz (2007) examined site tenacity (within season) and site fidelity (between years) for Le Conte's Sparrow during winter, and found evidence of site tenacity.

Knowledge of movement and spatial patterns of overwintering Le Conte's Sparrows is important for conservation planning and management of coastal prairies. For example, the optimal burning period in coastal prairies occurs during winter when Le Conte's Sparrows may be sedentary and site faithful. The objectives of our study were to: (1) radio-mark Le Conte's Sparrows to estimate home range size among burn years, (2) conduct monthly banding efforts to examine site tenacity, and (3) collect measurements of individual birds to compare body condition among burn years.

METHODS

Study Area.—This study was conducted during winter 2002–2003 at the Hoskins Mound Prairie, Brazoria National Wildlife Refuge (NWR), Texas. This area is part of the Texas Mid-Coast NWR Complex. Prior to its purchase in 1990, the land was used for rice farming and cattle ranching, which contributed to dissection of the refuge into numerous well-defined units surrounded by fire breaks, including levees, roads, and ditches. Units included in this study were those that appeared to have recovered from disturbances (J. B. Grace and L. K. Allain, pers. comm.; USGS, NWRC), probably due to adjacent seed banks. Dominant plant species in the study units included little bluestem (*Schizachyrium scoparium*), bushy bluestem (*Andropogon glomeratus*), saltmeadow cordgrass (*Spartina patens*), switchgrass (*Panicum virgatum*), cutover muhly (*Muhlenbergia expansa*), marsh elder (*Iva angustifolia*), longspike tridens (*Tridens strictus*), panicgrasses (*Dichanthelium* spp.), and flatsedges (*Cyperus* spp.). Saltbush (*Baccharis halimifolia*), a native and invasive shrub common in coastal areas, occurred in scattered clumps throughout much of the refuge, and dominated portions of many units included in this study. Other woody species included blackberries (*Rubus* spp.), Macartney rose (*Rosa bracteata*), wax myrtle (*Morella cerifera*), and Chinese tallow tree (*Triadica sebifera*).

Approximately 3,200 ha of Hoskins Mound Prairie are managed with prescribed burning. The burning program at this area was established in 1997 with emphasis on growing-season fires. Mowing and haying also have been used for management in some areas. The overall management plan for the entire refuge and Hoskins Mound includes an average burn rotation of 3–5 years, depending on site conditions and successional status. Most of the refuge is in compliance with this burn cycle, although weather conditions may impede implementation of scheduled burns in some years. Management is directed by general objectives and guided by periodic monitoring of habitat conditions.

Le Conte's Sparrow numbers on Christmas Bird Counts on Brazoria (Freeport) or San Bernard NWRs have been among the highest in the country (National Audubon Society 2002). The area provided an excellent opportunity to study Le Conte's Sparrow's home-range size and site tenacity during the winter.

We sampled replicate burn units subjected to a discrete set of burn intervals. Sample units were selected from those available using a completely randomized design. Each unit included was selected from all possible prairie units on Hoskins Mound Prairie, and burned within 1, 2 or 3 years of the initiation of data collection. We collected data from 15 burn units with five replicate units from each burn interval. Selected management units ranged in size from 40 to 520 ha. Banding sites were randomly selected for each unit in an area 50–500 m from the edge of the unit. Birds were radiomarked only on 1- and 2-year burn units.

Telemetry.—Le Conte's Sparrows were captured and radiomarked in five 1-year and five 2-year burn units during January and February 2003. Searching for birds to radiomark began from a random location at least 100 m from each unit boundary. Searchers moved from the edge of the unit until a bird was located and captured. Later in the season, due to limited access to some previously selected areas and time constraints, searching for birds to radiomark began from a non-random location at least 100 m from the unit boundary. Searches for a second bird on a unit

began at least 250 m from the first bird to reduce the chance of observer disturbance.

Each week, four birds, two from a 1-year and two from a 2-year burn unit were captured and radiomarked. A crew of 3–6 people located birds by walking in a line and flushing birds using poles and drag-lines. When a Le Conte's Sparrow was located, a 12-m mist-net was set up downwind from the bird, and the crew formed a semicircle behind the bird. The crew then rushed toward the net in an attempt to direct the bird into the net. This was repeated until a bird was netted.

Each bird was fitted with a 0.48-g radio transmitter (Model LB-2; 10-day battery life with an operating frequency near 165 MHz; Holohil Systems Ltd., Carp, ON, Canada) by placing it over the feathers of the synsacrum and attaching it with an elastic leg-loop harness (Rappole and Tipton 1991). Extra steps were taken to prepare transmitters for application due to the wet, salty conditions and dense herbaceous vegetation of coastal prairie. A rain event occurred after the second application of transmitters, and signals became weak, inconsistent or nonexistent. We retrieved one of the censored radios, and found antennas were rusting. Transmitter antennas were coated with epoxy following this incident in an attempt to resolve this problem. A bird was found entangled in the grass on one occasion. The transmitter was immediately removed and the bird was released alive. We removed 2.5 cm of the transmitter antenna after this incident and thereafter before deployment. Change in transmission signal as a result of this modification was negligible as predicted by Beeman et al. (2007).

Locations were recorded daily and every other day for a 1-hr period, until a mortality event occurred, the signal disappeared, or the bird was recaptured. Locations were established from an estimated distance of 25–100 m from the bird. Azimuth directions were recorded from two Global Positioning System points, 20–40 m apart. The radio-marked bird was located every 15 min for a 1-hr period (i.e., 4 locations/hr) to obtain an average location for that monitoring session. Recaptures of birds were attempted 6–11 days after capture to remove transmitters.

Banding.—Within-season site tenacity of wintering Le Conte's Sparrows was examined through monthly banding efforts. Birds were mist-netted monthly (Dec 2002–Feb 2003) on each burn unit (n = 15) on a 1-ha plot with the assistance of 10 or more volunteers. Plots consisted of a 100-m net lane with a 0.5-ha flushing zone on each side of the net. Plots were selected randomly. A 50-m buffer zone was maintained from roads and fire breaks. Vegetation was cut (~1 m wide) to create a path to allow the nets to stretch to the ground to deter birds from escaping under the net. Banding efforts began at sunrise and continued into early afternoon. Plots were netted in a different order each month.

Each captured bird was banded with an individually numbered aluminum federal leg band or their band number was recorded if recaptured. Wing chord (mm), fat score (scale 0–5), and mass (g) was recorded for each bird captured (Helms and Drury 1960, Krementz and Pendleton 1990). The same observer measured fat score on all birds to avoid observer bias. Birds were released where captured. Wind speed (km/hr), temperature (°C), and time of day also were recorded.

Analyses.—Telemetry data were analyzed using the Home Range Extension in ArcView 3.3 Geographic Information System (ESRI 2002) to estimate home-range size and activity centers using the kernel method (Worton 1989). Movement patterns were analyzed with the Animal Tracking Extension in ArcView. Home-range sizes were estimated at 50 and 95% probabilities. Differences among estimated home-range sizes were compared between 1- and 2-year burn treatments, and by mass of marked sparrows. Results were compared using PROC MIXED (SAS Institute 1999).

General information from banding data was derived and reported using program CAPTURE (White et al. 1978, Rexstad and Burnham 1991). Model M_b (behavioral response after capture) was selected as the most appropriate model for the data. The three parameters produced under model M_b were: N, estimated population size; P, the probability of capture of an unmarked animal on any trapping occasion; and c, the probability that an animal is captured on any trapping occasion subsequent to the occasion on which it was first captured (Zippin 1956, 1958; Otis et al. 1978). An index of body condition (IBC) was used to correct for variation associated with body mass. IBCs are residuals from a regression line of wing chord (independent variable) and body mass (dependent variable). IBC, fat score, and differences in recapture weight were analyzed using repeated measures analysis of variance (PROC MIXED; SAS Institute 1999).

RESULTS

Telemetry.—A total of 268 locations was obtained for birds monitored in 1-year burns and 236 locations in 2-year burns. Home-range estimates were produced for 18 of 26 birds radiomarked due to a minimum of 6 days of observations needed for analysis. Three of the 26 marked sparrows apparently detached from their transmitters, two were killed by predators (1 suspected avian, 1 unknown), one died of unknown causes, and nine were censored. Birds censored were those whose telemetry signal was lost and their fate was unknown. A radio was designated as detached if there was no evidence of predation (feathers, predator tracks or feces, etc.) or damage to the transmitter or antenna. Recaptured birds were tracked for an average of 9.5 days, and lost an average of 1.4 g (SE = 0.23) over the tracking period (Table 1). Transmitters were removed from 11 sparrows prior to the end of battery life.

Mean home-range estimates with 50 and 95% probability were 2.41 ha (median = 0.28 ha) and 10.31 ha (median = 1.27 ha), respectively (Table 1). Most birds limited their movements to locations within 200 m of their initial capture site, which is more clearly shown at the scale of the refuge (Fig. 1). The bird that moved the greatest distance was at an outlier location for 1 day. Removal of the day 8 location for bird # 289 reduced the 50% estimate of home range size from 20.91 to 0.08 ha, and 95% home range estimate from 86.3 to 0.51 ha. Two birds from different capture periods moved long distances and returned to their initial capture location the following day. Long-distance movements on day 3 inflated home-range estimates for birds # 280 and # 203. Removal of the single outlier location for bird #280 reduced the 50% estimate of home-range size from 4.50 to 1.54 ha, and 95% home-range estimate from 20.39 to 4.50 ha. The 50% home-range estimate for bird # 203 was inflated from 0.06 to 7.94 ha, and the 95% home-range estimate from 0.45 ha to 32.01 ha. Bird # 294 moved 509 m from its initial location and had somewhat nomadic behavior by remaining at the initial area for at least 5 days, then moved

TABLE 1. Home-range estimates (ha) at 50% and 95% probability for radio-marked Le Conte's Sparrows and mass differences (wtdiff) of recaptured birds. Fates are defined as: survived entire tracking period, censored, or loss of signal before end of tracking period, mortality, and transmitter detached.

Burn treatment	Identification #	Exposure days	Locations	50%	95%	wtdiff	Fate
1	196	4	2				Censored
	197	1	2				Transmitter detached
	202	7	27	0.03	0.14		Censored
	203	9	34	7.94	32.01	−1	Survived
	281	6	27	0.11	0.51	−1.3	Survived
	283	6	24	0.65	2.37	−2.2	Survived
	285	10	25	0.02	0.14	−1.3	Survived
	287	13	26	0.05	0.53		Censored
	291	10	20	0.21	0.93		Censored
	292	6	9	1.53	7.21		Censored
	318	10	39	0.31	1.51	−0.6	Survived
	319	11	33	0.43	2.19	−2.8	Survived
2	192	0	1				Survived
	193	10	39	0.4	2.39	−0.8	Survived
	194	1	2				Transmitter detached
	195	6	29	0.08	0.34		Mortality (unknown)
	199	5	8				Censored
	200	1	1				Censored
	205	2	3				Survived (grass entanglement)
	206	8	32	0.18	0.92		Censored
	279	8	32	0.16	1.04	−1	Survived
	280	12	34	4.5	20.39		Mortality (predation)
	288	1	2				Mortality (predation)
	289	8	23	20.91	86.3	−1.6	Survived
	294	10	21	5.82	26.01		Transmitter detached
	295	6	7	0.24	0.64		Censored

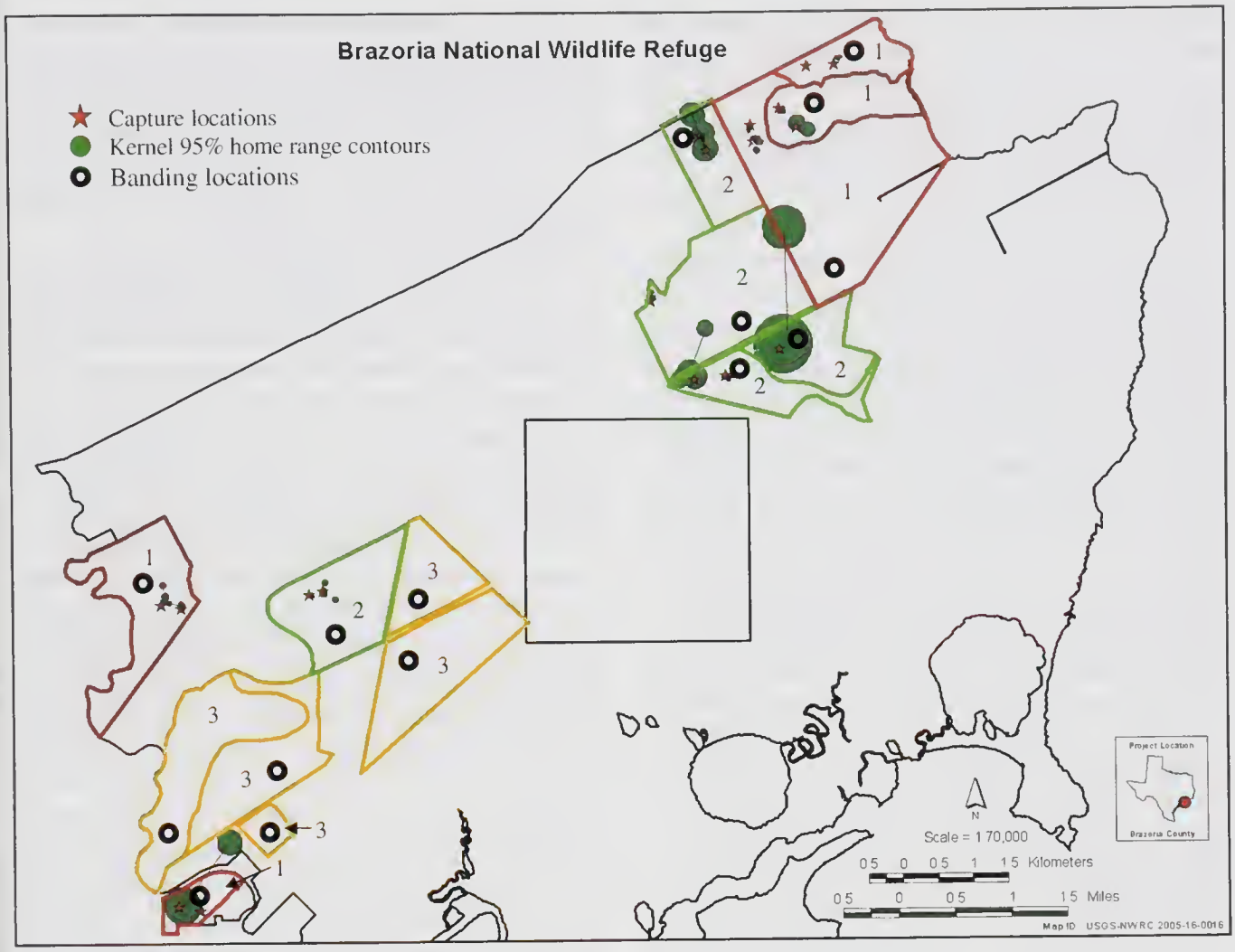

FIG. 1. Brazoria National Wildlife Refuge with 95% estimated home-range size of each radio-marked Le Conte's Sparrow indicated with gray circles. Black circles indicate monthly banding locations. Interior polygons represent burn unit boundaries burned within 1, 2, and 3 years.

~250 m for 1–2 days, and then an additional ~250 m from the initial location area for the final 2 days of monitoring (Table 1).

Burn year had no significant effect on home-range estimates at 50% ($P = 0.25$), 95% ($P = 0.23$), or mass loss of recaptured birds ($P = 0.46$). Month since burn had no significant effect on home-range estimates at 50% ($P = 0.40$), 95% ($P = 0.38$), or mass loss of recaptured birds ($P = 0.86$). Initial mass of birds was not correlated with home-range estimates at 50% ($P = 0.28$) or 95% ($P = 0.30$).

Banding.—A total of 103 Le Conte's Sparrows was captured on three trapping occasions (Dec, $n = 54$; Jan, $n = 34$; Feb, $n = 15$). Eight individuals were recaptured and no bird was recaptured more than once. Goodness of fit tests in program CAPTURE revealed M_b as the best fit model ($\chi^2 = 1.55$, df = 2, $P = 0.46$). Model M_b tests for a behavioral response after initial capture. Le Conte's Sparrow showed a significant behavioral response to capture ($P < 0.001$). Overall capture probability was estimated to be 0.462, while recapture probability was 0.056. Model M_b estimated that 122 (SE = 10.4) birds had all or part of their home ranges within 15 separate 1-ha plots. Burn treatment did not significantly influence overall fat score ($P = 0.85$), IBC ($P = 0.31$) or differences in recapture weights ($P = 0.83$).

DISCUSSION

Le Conte's Sparrows are primarily sedentary during winter and inhabit small home-ranges with most birds confining their movements to an area <2 ha. The extent to which site tenacity can be described was limited because of the small number of recaptures. Banding results contrasted with those from telemetry, suggesting that low recapture probability is likely due to avoidance of recapture and not movement from the area. This suggests that surveying birds in an area also with

banded birds might decrease their detection estimates due to avoidance behavior. Le Conte's Sparrows were studied throughout much of the winter, but each individual was tracked for a relatively short period of time, limiting our ability to draw conclusions about their behavior throughout the entire winter season.

Previous findings suggest that habitat selection of grassland birds is related to vegetation structure (Pulliam and Mills 1977, Igl and Ballard 1999, Baldwin et al. 2007) and food abundance (Tucker and Robinson 2003). If birds inhabit an area with sufficient cover and food, nomadic movements may be unnecessary, and survival is likely enhanced by familiarity with the area (Sinclair 1984, Gordon 2000). There also may be a tendency for solitary behavior. Grzybowski (1983) found Le Conte's, Grasshopper (*Ammodramus savannarum*), and Baird's (*A. bairdii*) sparrows tended to be solitary and avoided other individuals when flushed from adjacent locations. Le Conte's Sparrows also were suspected to inhabit restricted home ranges (Grzybowski 1983). Gordon (2000) reported Grasshopper, Baird's, Savannah (*Passerculus sandwichensis*), and Vesper (*Pooecetes gramineus*) sparrows remained within fixed home ranges in winter with Grasshopper Sparrows being the most sedentary. Le Conte's Sparrow did not occur in Gordon's (2000) study area.

Grzybowski (1983) examined space use of Le Conte's Sparrow and estimated that individuals were spaced 11–45 m apart leading him to speculate the species maintains small home ranges. Cooper (1984) found that Le Conte's Sparrows maintained a territory size of about 1.0 ha. Results from both studies were based on unmarked Le Conte's Sparrows. Estimates of home-range or territory size of Le Conte's Sparrows from both studies are similar to our findings.

Our radio-marked Le Conte's Sparrows consistently lost mass but we believe movement was not significantly impacted. Efforts to recapture radio-marked birds revealed them to be highly mobile. Loss of mass may be attributed to the induced stress of carrying the transmitter or associated with capture. The transmitter may have increased the resources needed for thermoregulation, although no evidence was recorded to support this hypothesis. Radio-marked birds carried transmitters that were <4% of their body mass (Federal Bird Banding Permit # 22207, 09/07/06–07/31//09).

Burn year and/or bird morphology revealed no relation to home-range size. Le Conte's Sparrows, in coastal prairies, are more abundant in areas that have been burned within 1 to 2 years versus 3 years (Baldwin et al. 2007), and both 1- and 2-year burn treatments likely provide suitable habitat for Le Conte's Sparrows.

Mark-recapture methods have improved and are used in numerous studies, but estimates of site tenacity in our study were hampered by the small number of recaptures. We were able to perform a test among general models in program CAPTURE, under closed population assumptions, and the results suggest Le Conte's Sparrows may exhibit a significant behavioral response to capture (M_b). It is difficult to distinguish between capture avoidance, poor survival and/or emigration; selection of model M_b may be confounded if emigration does occur (i.e., in an open population) but is not detected (Otis et al. 1978). Analysis using open population models was not successful due to insufficient data. Telemetry results (home-range size <2 ha), selection of model M_b, and an estimated density ($\pm$ SE) of 4.91 $\pm$ 1.49 birds/ha (Baldwin et. al. 2007) combined suggest that Le Conte's Sparrow home-ranges during the winter may overlap extensively, or that individuals remain fairly sedentary for an undetermined time (>10 days), and periodically move to other areas with suitable habitat.

Le Conte's Sparrow may exhibit site fidelity in wintering areas. Preliminary banding of Le Conte's Sparrows was conducted in January 2002 on one burn unit. A mist net was randomly placed in the same unit in January 2003, and one of the 84 Le Conte's Sparrows banded the previous year was recaptured less than 90 m from its original capture site.

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PATERNAL SONG COMPLEXITY PREDICTS OFFSPRING SEX RATIOS CLOSE TO FLEDGING, BUT NOT HATCHING, IN SONG SPARROWS

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ABSTRACT.—Sex allocation theory predicts that population sex ratios should be generally stable and close to unity, but individuals may benefit by adjusting the sex ratio of their offspring. For example, females paired with attractive males may benefit by overproducing sons relative to daughters, as sons inherit their fathers' attractive ornaments (''sexy son'' hypothesis). Similarly, if compatible gene effects on fitness are more pronounced in males than females, genetically dissimilar mated pairs may enhance fitness by overproducing sons (''outbred son'' hypothesis). We tested these hypotheses in Song Sparrows (*Melospiza melodia*) by examining offspring sex ratios of 64 complete families shortly after hatching (''early-stage'') and again shortly before fledging (''late-stage'') in relation to paternal song complexity and the genetic similarity of social mates. Neither early nor late-stage offspring sex ratio was related to parental genetic similarity. Nests of males with larger song repertoires contained more male-biased broods by the late-stage nestling period, but not in the early-stage nestling period. These findings suggest that attractive males may be better able to successfully raise male-biased broods, but not that females adaptively adjust primary sex ratios in response to their social mate's attractiveness. *Received 20 April 2009. Accepted 24 July 2009.*

Sex allocation theory predicts that population sex ratios tend to be stable and close to 1:1 (Fisher 1930), but variation among individuals in circumstances and quality may favor parents facultatively adjusting the sex ratios of their offspring (Trivers and Willard 1973). The ''sexy son'' hypothesis (Weatherhead and Robertson 1979), originally postulated to explain female tolerance for polygyny, also predicts that attractive males and their mates should produce predominantly sons, as sons may inherit elaborate ornaments. Consistent with this hypothesis, paternal attractiveness has been linked to offspring sex ratios in some birds (Ellegren et al. 1996) although not in others (Westerdahl et al. 1997; see analyses by Ewen et al. 2004, and also Cassey et al. 2006). These mixed results may indicate mechanistic constraints preventing some species from manipulating sex ratios, and/or a relatively weak selective advantage to doing so (Komdeur and Pen 2002, Fawcett et al. 2007). The question of how paternal attractiveness should affect offspring sex ratios in the case of sexually selected traits that are learned and/or highly environment-dependent, such as bird song, remains almost entirely unanswered (but see Leitner et al. 2006).

Good genes models of sexual selection have recently expanded to consider nonadditive, or compatible-gene effects on fitness (Neff and Pitcher 2005) with particular emphasis on heterozygote advantage. Compatible-gene effects are often observed in the expression of secondary sexual traits (Marshall et al. 2003, Reid et al. 2005), raising the possibility that sons may profit more than daughters from parental genetic compatibility. These effects are also commonly implicated in immunocompetence (e.g., Reid et al. 2005); this trait is expressed by male and females, but may affect male fitness disproportionately due to the immunosuppressive effects of high levels of circulating testosterone (Folstad and Karter 1992). If compatible-gene effects on fitness are stronger in males, optimal offspring sex ratios may depend in part upon parental genetic similarity. We refer to this possibility as the ''outbred son'' hypothesis.

Our objective was to examine if offspring sex ratios in Song Sparrows (*Melospiza melodia*) are associated with paternal attractiveness based on a learned trait (song repertoire size) and/or with parental genetic similarity. The mechanisms by which birds might manipulate offspring sex ratios comprise two major classes: before hatching, for example through selectively developing Z- or W-bearing ova; and after hatching, for example through preferentially feeding either males or females (Pike and Petrie 2003). We investigated sex ratios at two different points in the nesting cycle, once shortly after hatching and again shortly before fledging. Female Song Sparrows prefer males with more complex song repertoires (Searcy 1984, Reid et al. 2004), and song repertoire size has been correlated with immuno-

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competence, territory defense, and other measures of male fitness (Reid et al. 2005, Pfaff et al. 2007). Thus, the "sexy son" hypothesis predicts that males with larger repertoires (more attractive males) should produce male-biased broods. The "outbred son" hypothesis predicts that genetically dissimilar mated pairs should also produce male-biased broods, because individual genetic diversity is related both to immunocompetence and to repertoire size in this species (Reid et al. 2005).

METHODS

Study Subjects and General Field Methods.—We examined offspring sex ratios in 64 families of Song Sparrows breeding near Newboro, Ontario, Canada (44° 38′ N, 76° 19′ W). We captured adults in seed-baited treadle traps in April and May 2006, 2007, and 2008, outfitted each with a unique combination of colored leg bands, and collected a small (<25 μL) blood sample for genetic analysis. We identified mated pairs and located nests by behavioral observations. Each adult was included only once in the analysis; for birds that bred in multiple years we randomly selected which year's nest to include in the analysis. We included only first nesting attempts to reduce potential seasonal effects on sex ratio.

We collected a small (15 mL) blood sample from each nestling via femoral venipuncture 2 days after eggs hatched for subsequent genetic identification as male or female. We used felt-tip markers to mark nestlings' toes to track subsequent survival, weighed individuals to the nearest 0.1 g, and collected any unhatched eggs for genetic identification of inviable embryos as male or female. We returned to the nest 4 days later (6 days after hatching), noted which individuals were still present, and weighed each individual to the nearest 0.5 g. Day 6 was used to avoid artificially inducing early fledging, which normally occurs 8–10 days after hatching (pers. obs.).

Song Analysis.—We recorded songs of adult males early in the mating season onto Marantz Professional PMD 671 solid state recorders using Telinga Twin Science Pro parabolic microphones. We considered a repertoire to have been sampled in full after recording 300 consecutive or 450 non-consecutive songs following the guidelines established for this population by Pfaff et al. (2007). We generated spectrograms in SYRINX (John Burt, www.syrinxpc.com), and classified song types by visual inspection and sorting to identify each male's repertoire size. This was done blind with respect to offspring sex ratios.

Genetic Analysis.—We genotyped all adults at seven microsatellite loci: Escm 1 (Hanotte et al. 1994), Mme 2 and 7 (Jeffrey et al. 2001), Pdom 5 (Griffith et al. 1999), and Sosp 3, 13, and 14 (L. F. Keller, pers. comm.). We tested for deviations from Hardy-Weinberg expectations and from linkage equilibrium using GENEPOP Version 3.3 (Raymond and Rousset 1995), and found no evidence for either. We used microsatellite profiles to calculate Wang's (2002) coefficient of genetic similarity for each mated pair using MARK (Kermit Ritland, http://genetics.forestry.ubc.ca/ritland/programs.html).

We identified 208 nestlings and unhatched embryos from 55 nests (33 of which had survived to 6 days after hatching) as males or females over 3 years of study. We used primers P2 and P8 (Griffiths et al. 1998) to amplify portions of the CHD-W and CHD-Z gene, located on avian sex chromosomes. Each gel included control amplifications from a known male and a known female.

Statistical Analysis.—We investigated the relationships between offspring sex ratios and paternal repertoire size and/or parental genetic similarity using generalized linear models (GLM: PROC GENMOD) (SAS 2004) with a logit-link function and binomial error distribution. Embryos collected from unhatched eggs were included in the early-stage (2 days after hatching) analyses, while late-stage analyses included only nestlings that survived until 6 days after hatching.

We constructed two statistical models for both early and late-stage sex ratios. Initial models included paternal repertoire size, parental genetic similarity (using Wang's [2002] coefficient), year, and relative hatching date (number of days before or after the mean hatching date for all first-brood nests that year) as predictor variables. Final models excluded any clearly non-informative predictor variables ($\chi^2 < 1$). Number of sons within a nest for all models was the response variable and number of offspring (sons plus daughters) was the binomial denominator. All predictor variables were normally distributed (Kolmogorov-Smirnov test) and all statistical tests were two-tailed.

We tested whether the use of color bands might confound sex ratios in our study population, because colored leg bands may affect attractive-

ness and offspring sex ratios in some species (Burley 1986; but see Rutstein et al. 2005). We investigated the relationship between offspring sex ratio and the number of bands of that color on each adult male for each of the eight band colors using Pearson's correlations with the appropriate Bonferroni corrections. We did not observe any relationship between color bands and either hatching or fledging sex ratios (all $P > 0.05$), suggesting our use of colored leg bands was unlikely to be an important confounding issue in this study.

RESULTS

Fifty-four (53.8) percent (112 of 208) of nestlings analyzed 2 days after hatching were male. Sixty (55%) of the 109 nestlings that survived until at least 6 days after hatching were male. Our initial GLM identified a significant effect of year on early-stage offspring sex ratios ($\chi^2 = 6.01$, $P = 0.014$) with sex ratios somewhat more male-biased in 2007 than other years. None of the other predictor variables included in this model explained a significant amount of variation in early-stage offspring sex ratios (repertoire size: $\chi^2 = 0.34$, $P = 0.56$; parental genetic similarity: $\chi^2 = 0.25$, $P = 0.56$; relative hatching date: $\chi^2 = 0.13$, $P = 0.72$). Our initial GLM at 6 days after hatching identified a near-significant association between paternal repertoire size and offspring sex ratios ($\chi^2 = 3.28$, $P = 0.070$), and no significant effects of other predictor variables on late-stage sex ratios (parental genetic similarity: $\chi^2 = 0.77$, $P = 0.38$; relative hatching date: $\chi^2 = 0.77$, $P = 0.38$; year: $\chi^2 = 1.55$, $P = 0.27$). Our final GLMs included only repertoire size and year as predictor variables, and indicated a significant positive relationship between repertoire size and late-stage ($\chi^2 = 4.66$, $P = 0.030$) but not early-stage ($\chi^2 = 0.52$, $P = 0.47$) offspring sex ratios (Fig. 1).

Differences in sex ratios at day 6 could be explained by one of two possibilities: either there was increased mortality of female nestlings in attractive males' nests (creating a male bias), or there was increased mortality of male nestlings in less attractive males' nests (creating a female bias). Twelve of the thirty-three nests (36%) that had at least one nestling survive to day 6 (surviving nests) had partial brood loss. We used a *t*-test to investigate differences between the social fathers' repertoire sizes for nests in which male and female nestlings were dying, and found that daughters were consistently dying in nests of males with larger repertoire sizes ($t = -3.78$, df $= 64$, $P < 0.001$). The total number of offspring surviving to day 6 was not significantly correlated with social father's repertoire size ($r^2 = 0.003$, df $= 34$, $P = 0.763$). However, when analyzing predictors of number of nestlings lost in surviving nests, social father's repertoire size had a significant effect ($\chi^2 = 20$, $P = 0.002$).

We also compared the average growth rates of brothers to the average growth rates of sisters in the same nest to help explain differences in mortality. Brothers consistently grew faster than sisters ($t = -2.88$, df $= 20$, $P = 0.009$). The data indicate, although there was not sufficient statistical power to compare nestling mortality rates between years, that female mortality in surviving nests was higher than male mortality in surviving nests for 2 of the 3 years (Tables 1–2).

DISCUSSION

Offspring sex ratios near the end of the nestling period were significantly related to paternal song repertoire size (Fig. 1B), consistent with the predictions of the "sexy son" hypothesis. However, this relationship did not appear to be mediated through manipulation of primary sex ratios, as repertoire size did not predict sex ratios earlier in the nestling period (Fig. 1A). It is unlikely the lack of a relationship between song repertoire size and early-stage sex ratios was due to low statistical power, as we were able to detect an effect of repertoire on late-stage sex ratios despite a lower sample size of surviving nests (38 vs. 66). Adjusting primary sex ratios is presumably less costly in terms of fitness than altering sex ratios after hatching, but the apparent absence of primary sex-ratio manipulation may reflect an inability to do so.

The positive relationship between paternal song repertoire size and brood sex ratio late in the nestling period may or may not represent adaptive post-hatching male/female allocation. It remains to be learned whether adult Song Sparrows preferentially feed male or female offspring, much less how such biases might relate to paternal attractiveness. A growing body of evidence points to the importance of early developmental condition in shaping song-learning ability (e.g., Buchanan et al. 2003), suggesting that complex singers and their mates may benefit from overproducing, or preferentially feeding sons, if sons stand to gain more than daughters from direct benefits via increased paternal care. Secondary

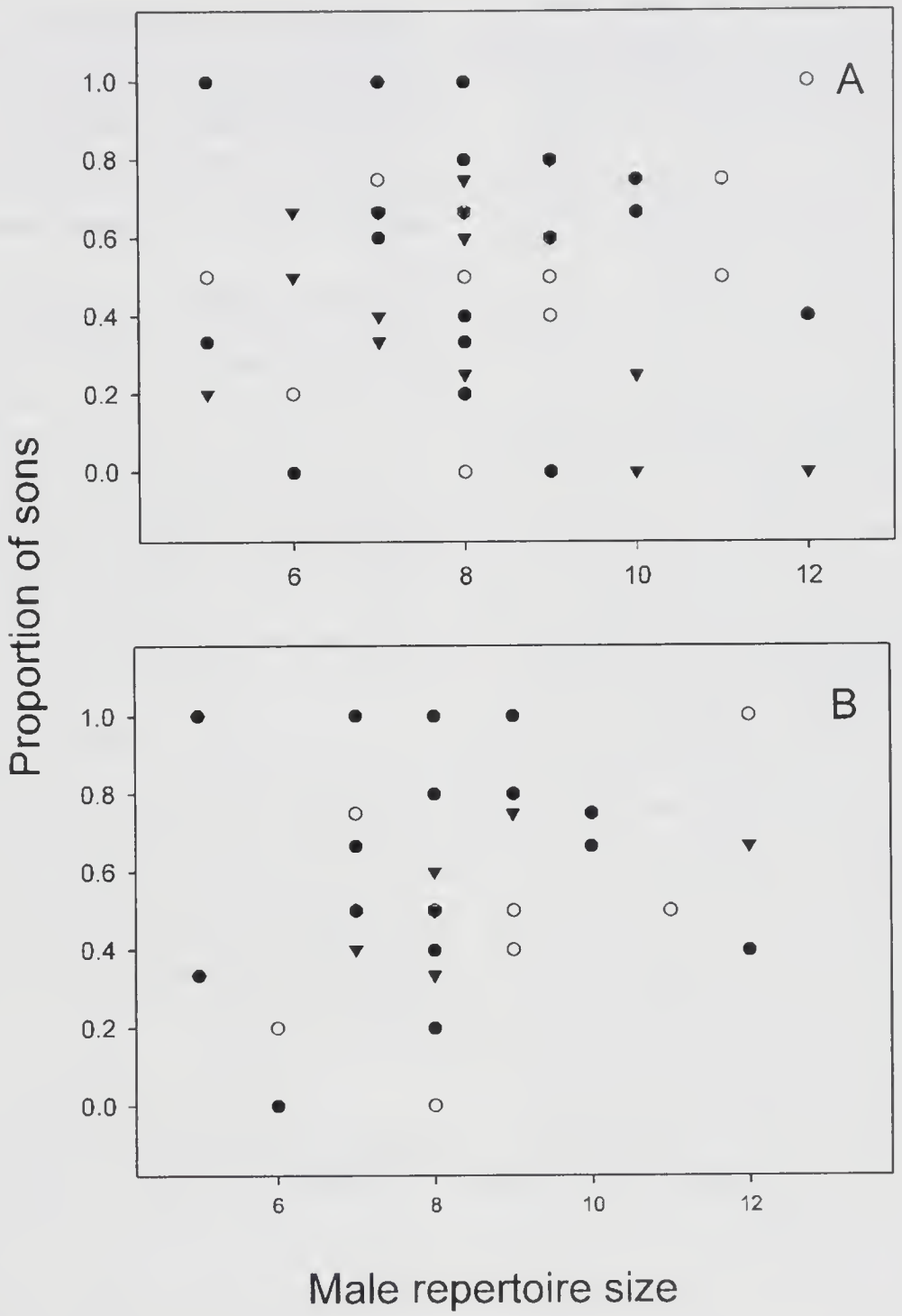

FIG. 1. Relationship between paternal repertoire size and offspring sex ratio, measured as proportion of sons, (A) 2 days and (B) 6 days after hatch over 3 years (filled circles = 2006, open circles = 2007, and inverted triangles = 2008).

TABLE 1. Population-wide nestling survival of Song Sparrows near Newboro, Ontario, Canada.

	2006		2007		2008	
	Males	Females	Males	Females	Males	Females
Day 2	59	35	26	26	27	35
Day 6	35	22	15	18	10	8
Survival rate	59%	63%	58%	69%	37%	23%

sexual traits in many species honestly advertise paternal ability or effort (Buchanan and Catchpole 2000, Voltura et al. 2002, Siefferman and Hill 2003). Thus, more attractive males would provision at a higher rate, resulting in a more noticeable difference between male and female sibling growth rates in nests of more attractive males. We observed a difference in growth rates between brother and sister nestlings, consistent with biased feeding.

TABLE 2. Population-wide nestling survival of Song Sparrows near Newboro, Ontario, Canada, including only nests in which at least one nestling survived to day 6.

	2006		2007		2008	
	Males	Females	Males	Females	Males	Females
Day 2	36	26	15	18	15	11
Day 6	35	22	15	18	10	8
Survival rate	97%	85%	100%	100%	80%	72%

Comparing mortality rates between female and male nestlings indicates the observed relationship between paternal repertoire size and sex ratios near fledging may be due to disproportionate mortality of daughters in the nests of attractive males. The reason for these female-biased deaths is not completely clear. One possibility is that male nestlings that are fed more often, perhaps by an attractive male, may be better able to outcompete their sisters. There may be a positive feedback effect whereby an increase in the size of a male nestling may enhance his begging ability, resulting in further biased feeding from parents. Consistent with this possibility, female Song Sparrow nestlings in nests parasitized by Brown-headed Cowbirds (*Molothrus ater*) are more susceptible to being outcompeted by the faster-growing cowbird nestling (Zanette et al. 2005). This could be interpreted as an adaptive sex ratio bias in that sons may be preferentially fed; however, the deaths of female nestlings could be an "unintended" result of this feedback effect.

We cannot rule out effects of disease and partial predation, but starvation resulting from differential provisioning by parents is likely the main cause of partial brood reduction, as theorized by Ricklefs (1969), and supported by experiments by Arcese and Smith (1988) and observations by Hochachka and Smith (1991). Nestling growth rate in this population is correlated with parental visits, providing further support to the theory that nestling success is heavily influenced by parental care (Potvin and MacDougall-Shackleton 2009).

We observed no relationship between parental genetic similarity and offspring sex ratio, contrary to the predictions of the "outbred son" hypothesis. This may reflect low statistical power, an inability to detect genetic compatibility, and/or a relatively weak selective advantage to adjusting sex ratios in response to this variable. Some traits exhibiting heterozygote advantage are expressed mainly by males, such as song-learning ability (Marshall et al. 2003, Reid et al. 2005), but genetic diversity can also enhance female fitness, for example through fecundity (Ortego et al. 2007) and hatching success (Marr et al. 2006). There may be little, if any, selective advantage to manipulating primary or secondary brood sex ratios in response to expected offspring heterozygosity.

Adaptive adjustments to primary sex ratios appear taxonomically widespread among birds, but our study adds to a growing body of evidence that the pattern is by no means universal (Komdeur and Pen 2002, Ewen et al. 2004, Cassey et al. 2006). Moreover, apparently adaptive patterns of variation in secondary sex ratios may represent a byproduct of environmental conditions and the quality of care provided by attractive versus less attractive males, rather than a facultative response by females to the perceived attractiveness of their mates.

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INFLUENCE OF AGE AND SEASON ON MORPHOMETRIC MEASUREMENTS OF THE BISCUTATE SWIFT (*STREPTOPROCNE BISCUTATA*)

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ABSTRACT.—Little emphasis has been placed on the influence of season and age on morphological measurements of swifts, which makes comparative mensural studies difficult in the Apodidae. This study provides information about the importance of morphological variation in measurements to the biology of the Biscutate Swift (*Streptoprocne biscutata*). I studied individuals captured at four colonies in southern Brazil. Mass varied with age, time of day, and season. Birds captured at dawn weighed 115.5 ± 9.9 g (n = 1,320). Mass was greater in fall and spring and lower in summer and winter. Subadults weighed less than adults during summer, fall, and winter. The wing measured 206.3 ± 5.2 mm (n = 812), and the tail measured 69.9 ± 4.6 mm (n = 802); both showed seasonal variation in length. The tarsus measured 25.9 ± 0.6 mm (n = 695), and the exposed culmen measured 9.94 ± 0.36 mm (n = 658). The Biscutate Swift has significant seasonal variation in several morphological measurements. This variation should be considered in studies comparing populations of this species, as well as those of other apodids. *Received 6 April 2009. Accepted 4 September 2009.*

The morphology of the Apodidae is conservative and they are remarkably uniform in many respects, such that differences among them are subtle and may even be undetectable in prepared skins. Some species of the genera *Cypseloides*, *Aerodramus*, *Chaetura*, and *Apus* are not easily distinguished even when observed in the hand (Wetmore 1957; Sims 1961; Medway 1966; Chantler and Driessens 1995; Chantler 1995, 1999). Swifts do not vary greatly in size interspecifically, and only minor differences are apparent in the shape of the beak, tail, wing, and tarsus. Morphological measurements, in some cases, contribute to diagnoses of species and subspecies (e.g., Sick 1991, Marín and Stiles 1992, Browning 1993, Parkes 1993, Chantler and Driessens 1995). Clinal variations, at times, lead to high numbers of subspecies, although not all variations justify taxonomic separation (Chantler and Driessens 1995).

The body mass of many swifts also depends upon age and season, and variations are much greater than those in passerine birds of the same size (Lack and Lack 1951, Naik and Naik 1966). Subadults in some species weigh less than adults during part of the first year of life, and this feature is used to estimate the age of individuals (Coffey 1958, Collins 1968, Tella et al. 1995). However, several studies that made morphological comparisons among species did not consider possible variation in measurements caused by environmental and age-related factors. Sick (1991) based the diagnosis of *Streptoprocne biscutata seridoensis* on differences in body mass and wing and tail length, but did not consider seasonal variation. Some descriptions of new *Cypseloides* species also ignored variation in measurements throughout the year (Eisenmann and Lehmann 1962, Collins 1972, Navarro et al. 1992). Taxonomists have used the data available and, considering the scarcity of museum material and the difficulty of studying swifts, those surveys have helped us to understand species relationships. However, little emphasis has been placed on the seasonal and age dependency of some measurements. This tendency can make comparative population studies difficult. I investigated age-related and seasonal variation in morphological measurements at four colonies of the Biscutate Swift (*Streptoprocne biscutata*) in southern Brazil, and I discuss the results with regard to the use of those parameters in taxonomic studies.

METHODS

Four Biscutate Swift colonies were studied in the eastern part of the State of Paraná, southern Brazil (Anhangava colony, municipality of Quatro Barras – 25° 22′ S, 48° 58′ W, 1,250 m asl; Serra do Capivari colony, municipality of Campina Grande do Sul – 25° 11′ S, 48° 51′ W, 1,050 m asl; and Arenitos and Furna 1 colonies, municipality of Ponta Grossa – 25° 15′ S, 50° 00′ W, ~1,000 m asl; Fig. 1). Only measurements from captured individuals were used. Mist nets and other nets were used to capture swifts near the most frequently used exit of each cave or roost

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FIG. 1. Biscutate Swift colonies studied in southern Brazil. (A) Anhangava, municipality of Quatro Barras, (B) Capivari, municipality of Campina Grande do Sul, (C) Arenitos, and (D) Furna 1, both in the Vila Velha State Park, municipality of Ponta Grossa.

site (Pichorim and Monteiro-Filho 2010). Metallic numbered bands, supplied by CEMAVE/ICMBio, (4.5 mm inner diam) were used to mark captured swifts. The following measurements of each captured individual were taken: body mass, wing length (flattened and straightened), tail length (measuring with a metal ruler inserted between the central pair of rectrices), tarsus length, exposed culmen length (measured from the beak tip in a straight line to the edge of the feathers in the central part of the forehead), and length of beak from nostril (hereafter nostril beak tip; measured from the anterior end of the maxilla in a straight line to the anterior edge of the nostril). Pesola spring scales (300 g capacity; estimated to the nearest 1g), calipers (15 cm), and rulers (30 cm) were used to measure swifts. All birds were released near the place of capture.

Analysis of variance (ANOVA) and *t*-tests (*alpha* = 0.05) were used to test the hypothesis of the existence of only one group of means for measurements taken during different seasons, age classes, and colonies following Zar (1984). Normality of distribution was tested for each comparison, and variances were considered analogous if one did not exceed double of the other. Measurement sets with samples of similar sizes were compared by ANOVA and tested for normal distribution and homogeneity of the variances using Bartlett, Brown-Forsythe, and Levene tests (JMP 4.0.4, SAS 2001). Data are presented as means ± SD. Individuals younger than 1 year of age were considered subadults. Age could be ascertained for marked nestlings captured after leaving the nest, and for individuals captured without molt of remiges and rectrices between January and March, the months in which all adults molt (pers. obs.).

RESULTS

Adult swifts weighed 115.7 ± 9.9 g (n = 1,340); considering only birds captured at dawn, the mass was 115.5 ± 9.9 g (n = 1,320). The heaviest individual (153 g) was captured in Arenitos on the afternoon of 2 September 2001. This individual had been captured the previous year at dawn on 14 October 2000 and weighed 125 g. The lightest individuals (87 g, n = 2) were captured in Arenitos on 2 December 2000. The plumage of these birds did not allow estimation of their age. However, subadults weighed less than adults captured in the same period. Adults in summer (Jan–Mar) weighed 110.9 ± 6.8 g (n = 292), while subadults weighed 102.5 ± 9.3 g (n = 8) (t = 3.43, df = 298, $P < 0.001$). Adults in fall (Apr–Jun) weighed 118.9 ± 6.7 g (n = 128), and subadults weighed 111.0 ± 10.4 g (n = 5) (t = 2.54, df = 131, P = 0.012). Adults in winter (Jul–Sep) weighed 116.1 ± 10.5 g (n = 456), and subadults weighed 97.7 ± 11.5 g (n = 6) (t = 4.28, df = 460, $P < 0.001$). Adults in spring (Oct–Dec) weighed 116.9 ± 10.4 g (n = 444), and subadults weighed 108.8 ± 4.2 g (n = 6) (t = 1.88, df = 448, P = 0.061). The lightest confirmed subadult (86.0 g) was captured at dawn on 9 July 2002 in Arenitos.

No differences in mass were apparent between males and females, as measurement of adults by season had a normal distribution. The mass of birds captured at dawn varied during the year; birds weighed more in fall and spring and less in summer and winter. Analyzing random samples of the same size from each season confirmed these

differences (ANOVA $F_{3,396} = 19.8$, $P < 0.001$). Adults were heavier in September and lighter in February (124.0 ± 8.7 g, $n = 105$ and 108.0 ± 5.2 g, $n = 35$; Table 1). Seasonal variation in mass was noted in some individuals captured repeatedly. An individual weighing 139 g was captured in the Anhangava colony on 11 October 1994, and the same individual weighed 104 g on 24 February 1995. This variation corresponds to a loss in mass of 25% in a 4-month period. Two other individuals, both captured in Arenitos, had mass changes of 30 g in a few months. The first individual weighed 138 g on 13 October 2000 and 108 g on 12 December (a 22% decrease). The second individual weighed 101 g on 12 December 2000 and 131 g on 3 September 2001 (a 30% increase). These values were not related to time of capture, as all individuals were weighed at dawn as they were leaving the night roost.

Variations in mass were also observed in individuals captured at day's end. The maximum variation was 15 g, for an individual from the Capivari colony, captured on 24 November 2000 weighing 131 g and recaptured the following day weighing 116 g (a 12% decrease). Six birds captured at day's end had mass decrease of 9–13 g (a 7–10% decrease). Sixteen of 25 birds captured at day's end had mass decreases, six had mass increases (not more than 5 g), and three had no variation. An individual captured in Capivari at 0615 hrs on 27 October 2001 weighed 111 g, and 109 g at 1000 hrs the same day, a 2 g decrease during a period of 3 hrs and 45 min. A nocturnal decrease of 17 g (13%) was observed for an individual captured on 24 November 2000 at Capivari colony; it weighed 131 g in late afternoon and 114 g the following morning.

The mean annual mass of adults captured at dawn varied among the colonies (Capivari = 120.2 ± 9.0 g, $n = 169$; Arenitos = 115.9 ± 10.1 g, $n = 610$; Anhangava = 113.7 ± 8.7 g, $n = 360$; and Furna 1 = 113.2 ± 7.8 g, $n = 181$). However, these data are not totally comparable because of seasonal variations of individuals captured in each colony. Considering only March, April, August, October, and November, when I obtained random samples of the same size from each colony, the Furna 1 average was smaller than

TABLE 1. Measurements of body mass, wing length, and tail length in adult *Streptoprocne biscutata* captured at dawn at four colonies in southern Brazil (Mean ± SD, *n*; minimum – median – maximum).

Month	Mass (g)	Flattened wing (mm)	Tail (mm)
Jan	108.1 ± 5.4, 134	203.6 ± 5.2, 134	66.6 ± 3.8, 99
	93.0–108.0–120.0	186.0–204.0–215.0	51.0–67.0–78.0
Feb	108.0 ± 5.2, 35	203.1 ± 6.9, 34	72.7 ± 2.5, 35[a]
	98.0–109.0–117.0	189.0–204.0–218.0	66.0–73.0–77.0
Mar	115.0 ± 6.6, 119	207.3 ± 7.3, 20	75.0 ± 2.5, 16
	98.0–115.0–132.0	184.0–209.0–217.0	70.0–75.0–79.0
Apr	118.5 ± 5.4, 78	200.7 ± 5.6, 59[b]	75.7 ± 2.82, 52
	106.0–119.0–134.0	185.0–201.0–214.0	68.0–76.0–83.0
May	122.8 ± 2.6, 5	207.8 ± 3.0, 5[c]	74.8 ± 1.9, 5
	120.0–122.0–126.0	205.0–207.0–211.0	72.0–75.0–77.0
Jun	122.3 ± 8.3, 96	207.8 ± 4.1, 96	76.0 ± 3.5, 96
	101.0–122.5–139.0	199.0–208.0–219.0	62.0–73.5–80.0
Jul	109.9 ± 8.1, 233	208.7 ± 3.9, 115	72.0 ± 3.0, 115
	90.0–110.0–135.0	198.0–209.0–218.0	64.0–72.0–80.0
Aug	119.4 ± 8.1, 62	208.2 ± 4.4, 62	70.3 ± 3.9, 62
	99.0–120.0–134.0	198.0–209.0–217.0	60.0–71.0–77.0
Sep	124.0 ± 8.7, 105	207.2 ± 4.0, 71	69.6 ± 3.6, 72
	107.0–125.0–141.0	197.0–208.0–218.0	60.0–70.0–78.0
Oct	120.7 ± 10.2, 217	206.7 ± 4.9, 132	67.6 ± 4.0, 135
	96.0–121.0–144.5	194.0–207.0–219.0	54.0–67.5–78.0
Nov	120.2 ± 7.4, 75	206.9 ± 4.8, 50	68.3 ± 2.6, 52
	100.0–122.0–134.0	192.0–207.0–214.0	62.0–68.0–73.0
Dec	109.6 ± 8.0, 161	204.2 ± 5.2, 98	67.7 ± 4.7, 98
	87.0–110.0–130.0	192.0–205.0–214.0	57.0–68.0–76.0

[a] Individuals molting rectrices (27 in the 1st and 2nd pair, 6 in the 1st pair, and 2 in the 2nd pair).
[b] Individuals molting primaries (33 in the 9th and 10th pair, 14 in the 9th pair, and 12 in the 10th pair).
[c] Individuals molting the 10th pair of primaries.

those of the other colonies (ANOVA $F_{3,314} = 5.6$, $P < 0.001$; $\text{mean}_{\text{Capivari}} = 120.8 \pm 8.3$ g, SE = 0.92, $n = 80$; $\text{mean}_{\text{Arenitos}} = 119.9 \pm 7.7$ g, SE = 0.86, $n = 80$; $\text{mean}_{\text{Anhangava}} = 119.5 \pm 8.6$ g, SE = 0.96, $n = 80$; $\text{mean}_{\text{Furna}} = 115.9 \pm 7.7$ g, SE = 0.87, $n = 78$; variances were homogeneous according to Bartlett, Brown-Forsythe, and Levene tests).

Of individuals captured that were not molting primary remiges 9 and 10, wing length was 206.3 ± 5.2 mm ($n = 812$). The longest wings measured 219 mm (bird captured in Anhangava colony on 11 October 1994 and another captured in Arenitos colony on 17 June 2001). The shortest wing measured 184 mm for a bird captured in Capivari on 2 March 2002 (this wing was severely worn). Generally, individuals without molt of the outer primary feathers, captured from January to March, showed wear on the tip of the primaries. As a result, the mean was smaller than during the rest of the year (203.9 ± 5.9 mm, $n = 188$). Wing length was 207.1 ± 4.7 mm ($n = 624$) between June and December. The largest monthly mean was in July (208.7 ± 3.9 mm, $n = 115$), and the smallest was in February (203.1 ± 6.9 mm; Table 1). Subadults did not have the same differences in means between the January–March period and the rest of the year ($\text{mean}_{\text{Jan–Mar}} = 203.2 \pm 4.4$ mm, $n = 9$; $\text{mean}_{\text{Apr–Dec}} = 201.6 \pm 3.7$ mm, $n = 18$) ($t = 0.99$, df = 25, $P = 0.33$). Wings of subadults measured 202.1 ± 4.0 mm (range 196.0–209.0 mm, $n = 27$). This value was not different from that for adult wings at the beginning of the year (Jan–Mar) ($t = 1.48$, df = 213, $P = 0.14$), but differed from the June–December period ($t = 5.33$, df = 649, $P < 0.001$). Mean wing length of adults in the June–December period had little variation among colonies (Capivari = 207.5 ± 4.8 mm, $n = 82$; Arenitos = 206.6 ± 4.7 mm, $n = 242$; Anhangava = 208.6 ± 4.1 mm, $n = 167$; Furna 1 = 205.7 ± 4.9 mm, $n = 133$). Considering similar random samples of the same period and size from each colony, wing length of birds from Furna 1 was smaller than in the other colonies (ANOVA $F_{3,168} = 11.44$, $P < 0.001$; variances were homogeneous according to Bartlett, Brown-Forsythe, and Levene tests).

Tail length of adults not molting the innermost feathers (first and second pairs of rectrices) was 69.9 ± 4.6 mm ($n = 802$). An individual captured at Furna 1 on 8 April 2001 had the longest tail (83.0 mm), while an individual captured in Anhangava on 19 January 1995 had the shortest tail (51.0 mm) with a worn tip and molt of rectrices 5–6 (outermost feathers). Individuals without molt of the first rectrices, captured from January to March, exhibited worn tail tips. The tail in this period was shorter than during the rest of the year ($\text{mean}_{\text{Jan–Mar}} = 67.8 \pm 4.7$ mm, $n = 116$; $\text{mean}_{\text{Apr–Dec}} = 70.3 \pm 4.5$ mm, $n = 685$) ($t = 5.38$, df = 799, $P < 0.001$). The largest monthly mean (76.0 ± 3.5 mm, $n = 96$) was in June and the smallest (66.6 ± 3.8 mm, $n = 99$) was in January (Table 1).

Tail lengths of subadults varied between 55.0 and 71.0 mm throughout the year, resulting in a mean of 65.4 ± 4.0 mm ($n = 27$). The birds had longer tails during January–March than during the rest of the year ($\text{mean}_{\text{Jan–Mar}} = 68.3 \pm 2.5$ mm, $n = 9$; $\text{mean}_{\text{Apr–Dec}} = 64.0 \pm 3.8$ mm, $n = 18$) ($t = 3.13$, df = 25, $P = 0.005$). Tails of adults in the second half of the year were longer than those of subadults ($t = 5.89$, df = 701, $P < 0.001$). Length of tails of adults in the period without molt of the rectrices (Apr–Dec) varied among colonies (Capivari = 68.0 ± 4.0 mm, $n = 95$; Furna 1 = 68.9 ± 5.1 mm, $n = 144$; Anhangava = 70.5 ± 3.4 mm, $n = 183$; Arenitos = 71.7 ± 4.4 mm, $n = 263$). Considering similar random samples of the same period and size from each colony, tail length of birds from Furna 1 was smaller than in the other colonies and larger than birds from Arenitos (ANOVA $F_{3,218} = 28.79$, $P < 0.001$).

The tarsus of adults measured 25.9 ± 0.6 mm ($n = 695$). An individual captured in Anhangava had the longest tarsus (27.5 mm), and two individuals from this colony and two from Furna 1 had the shortest tarsi (24.3 mm). The tarsus of subadults was 25.8 ± 0.5 mm (24.7–26.7 mm, $n = 24$), which did not differ from measurements of the adults ($t = 0.22$, df = 717, $P = 0.83$). The mean length of the tarsus of adults was similar among colonies (Furna 1 = 25.8 ± 0.6 mm, $n = 155$; Capivari = 25.8 ± 0.6 mm, $n = 108$; Anhangava = 25.8 ± 0.7 mm, $n = 114$; Arenitos = 25.9 ± 0.6 mm, $n = 318$) (ANOVA $F_{3,691} = 1.42$, $P = 0.24$; variances were homogeneous according to Bartlett, Brown-Forsythe, and Levene tests).

The exposed culmen of adults measured 9.94 ± 0.36 mm ($n = 658$). An individual captured in Arenitos had the longest exposed culmen (11.1 mm), and at least one specimen from each colony had the shortest exposed culmen (9.0 mm). Individuals with head feather molt had longer exposed culmens ($\text{mean}_{\text{with molt}} = 9.98 \pm$

0.34 mm, $n = 376$; $\text{mean}_{\text{without molt}} = 9.88 \pm 0.37$ mm, $n = 282$; $t = 3.40$, df = 656, $P < 0.001$). The nostril beak tip (mean = 6.27 ± 0.29 mm, $n = 658$) did not vary with molt ($\text{mean}_{\text{with molt}} = 6.29 \pm 0.28$ mm, $n = 376$; $\text{mean}_{\text{without molt}} = 6.24 \pm 0.32$ mm, $n = 282$) ($t = 1.95$, df = 656, $P = 0.052$). Subadults had exposed culmens similar to adults without molt ($\text{mean}_{\text{subadults}} = 10.07 \pm 0.29$ mm, $n = 15$; $t = 1.90$, df = 295, $P = 0.058$), but the nostril beak tip was shorter ($\text{mean}_{\text{subadult}} = 6.07 \pm 0.31$ mm, $n = 15$; $t = 2.09$, df = 295, $P = 0.037$). Considering the nostril beak tip measurement, which did not vary with molt, and random samples of similar size from each colony, individuals from Furna 1 had the shortest beak (Furna 1 = 6.19 ± 0.34 mm, $n = 100$; Capivari = 6.28 ± 0.26 mm, $n = 100$; Arenitos = 6.31 ± 0.27 mm, $n = 100$; Anhangava = 6.31 ± 0.30 mm, $n = 97$) (ANOVA $F_{3,393} = 3.66$, $P = 0.013$).

DISCUSSION

Body mass of Biscutate Swifts depended on time of day, age, and season. There was no evidence of differences in mass between males and females, a valid comparison as seasonal samples had normal distributions. Feeding was presumably the cause of daily mass variations, as individuals captured in late afternoon were heavier due to their digestive systems being full. Mass of subadults was lower than adults during the greatest part of the first year of life. The difference in mass was observed in summer, fall, and winter. Other subadult swifts have a similar tendency (e.g., Chimney Swift [*Chaetura pelagica*], Chapman's Swift [*C. chapmani*], and Alpine Swift [*Tachymarptis melba*]) (Coffey 1958, Collins 1968, Tella et al. 1995). Fat storage in nestlings increases their chances of survival after leaving the nest. However, young swifts probably experience some difficulty obtaining food during the first months of independent life. It is known that Biscutate Swifts decrease in mass between the nestling phase and the first months as subadults (Pichorim 2002). However, the new data demonstrate that mass of subadults is below that of adults for longer than previously known. It is likely that subadult survival during the first year of life is lower than for adults, as it is for some Apodidae (Chantler and Driessens 1995, Chantler 1999). Mass equalization between age groups occurs during the spring at the end of the first year of life. Reserves stored during the nestling phase appear to be indispensable for the survival of subadults. Control of brood size in the Biscutate Swift is achieved by egg ejection, probably during unfavorable conditions (Pichorim and Monteiro-Filho 2008). This behavior allows for heavier fledglings and, consequently, higher subadult survival during the first year.

Seasonal variation in the mass of adults may be related to prey availability, reproductive period, and molt with mass peaking in fall and spring, as observed for Chimney Swift (Coffey 1958, Johnston 1958) and Common Swift (*Apus apus*) (Lack and Lack 1951). The first period coincides with the end of molt when demand for energy is reduced. The new plumage may also act to increase mass, as it improves flight efficiency and facilitates capture of prey. It is also possible that storing of reserves before winter indicates an adaptation for low food availability. Increases in mass occur in spring due to increased resource availability and breeding. Mass starts decreasing by December, which is certainly related to the effort of caring for nestlings. The decrease in mass in summer is probably caused by the increased metabolic demand of molt. The maximum gain and loss of mass for the same individual in a year (30 and 25%, respectively) were close to rates for the Common Swift (31.3 and 13.2%, respectively (Lack and Lack 1951). The 13% overnight decrease in mass detected is the highest rate reported for Apodidae. The highest value previously reported for the Common Swift was 10% (Lack and Lack 1951).

Mass decrease of individuals captured in morning and at day's end could be linked to stress of capture. However, captured individuals were set free only after other individuals left the overnight shelter and were subsequently isolated from other individuals of the colony. Thus, the mass decrease could be an indication the species uses a technique of hunting for food in flocks and, when an individual is apart from the flock, it forages less efficiently. Schoener (1971) reports that grouping benefits animals when food availability fluctuates over time. This technique enlarges the monitored area and increases the chances of finding prey when resources are restricted or infrequent. Individuals may experience more difficulty in feeding when flying alone or in small flocks.

Seasonal variation of wing and tail lengths was mainly due to natural wear. Wings were shorter at the start of molt because the feathers were worn

from use. Mean lengths were greater after molt with the new plumage. Wings and tails of subadults were shorter than those of the adults, as subadults do not molt during the first year of life and have older feathers. The difference in tail lengths of subadults between summer and other periods of the year also appeared to be caused by wear.

There was no difference in tarsus length of adults and subadults. The tarsus of *S. biscutata* grows quickly during the nestling stage, reaching maximum development at the 19th day of life; this serves the nestlings well for hanging onto their nest (Pichorim 2002). Tarburton (1986) reported the tarsi of White-rumped Swiftlets (*Aerodramus spodiopydius assimilis*) in Fiji reached adult size on day 14, whereas adult weight was not reached until day 23 and wing-length sometime after fledging. Marín (1997) also showed the tarsus of *Cypseloides niger* reached adult length in about 12 days whereas mass took about 20 days and wing reached adult length post fledging. The tarsus is a good morphological measurement to compare populations due to its stability and quick development.

Molt of head feathers influenced the exposed culmen, which implied a certain limitation in using it as a comparison between populations that were not sampled during the same period. No plausible cause points to age-related variations of the nostril beak tip length, but the differences could be caused by increased cranial ossification or by the development of the beak.

Means of body mass and lengths of wings, tails, and nostril beak tip were significantly smaller in Furna 1. These data suggest that individuals from this colony experience special conditions, which may be related to competition for better places for resting, overnight roosting, and nesting with White-collared Swifts (*Streptoprocne zonaris*) (a large number of which inhabit the same shelter).

This study demonstrates that several morphological parameters of the Biscutate Swift have significant seasonal variations. There is evidence that similar variation occurs in other species of the Family Apodidae. Thus, studies to compare Apodidae populations must consider the dependence of certain morphological measurements on season and age. The existence of morphological differences over a latitudinal gradient is probable in some swifts. However, comparison of samples from different seasons could accentuate the differences between populations and lead to misinterpretation.

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Cooperative Breeding by Red-Headed Woodpeckers

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ABSTRACT.—Red-headed Woodpeckers (*Melanerpes erythrocephalus*) are one of the most easily recognizable bird species, but little is known about their social system and breeding activity due to their lack of sexual dimorphism. We observed a dense population of Red-headed Woodpeckers and found evidence of cooperative breeding. The habitat at our site may promote cooperative breeding because it has a high density of utility poles that woodpeckers use for nesting, roosting, and caching food. *Received 7 April 2009. Accepted 30 July 2009.*

Cooperative and communal breeding in which some individuals forgo breeding and assist other breeding pairs have been described for > 300 species of birds (Stacey and Koenig 1990, Cockburn 2003, Koenig and Dickinson 2004). Seven of 21 members of *Melanerpes* woodpeckers, including the Acorn Woodpecker (*M. formicivorus*) and Hispaniolan Woodpecker (*M. striatus*), are known to breed either cooperatively or communally (Koenig and Mumme 1987, Ligon and Burt 2004). Relatively little is known of the breeding behavior and social interactions of the Red-headed Woodpecker (*M. erythrocephalus*) as they are sexually monomorphic and difficult to capture (Smith et al. 2000). Anecdotal observations suggest Red-headed Woodpeckers may not be the monogamous loners as portrayed. They have been observed migrating in groups of 5–6 individuals suggesting they may remain in family groups for extended periods of time (Hall 1983), and three adults have been observed attending the same nest (Short 1982). These observations raise the possibility that some populations of Red-headed Woodpeckers may be cooperative breeders.

The objectives of our study were to: (1) observe a locally dense population of Red-headed Woodpeckers in west-central Illinois to better understand their social behaviors during the breeding season, and (2) examine if the dense population was a result of cooperative breeding or non-breeding floaters in the area.

METHODS

The study site was a 6.75-ha campground at Spring Lake Park (40° 50′ N, 90° 71′ W) in Macomb, Illinois, USA. The area was relatively open with the dominant vegetation being oak (*Quercus* spp.) and hickory (*Carya* spp.) trees with snags present throughout the area, in addition to 31 utility poles. Individual woodpeckers were captured in mist nets using call backs and mounted specimens, and banded with USGS bands and a unique combination of color bands. Fifteen Red-headed Woodpeckers were captured and banded. Red-headed Woodpeckers were observed during the 2007 and 2008 breeding seasons (late Mar through early Aug) to identify: (1) number of territories, (2) territory boundaries and whether territories overlapped, (3) color band combinations of marked individuals in each territory, (4) nest site locations, (5) number of birds and the identity of individuals tending a nest, and (6) number of birds and the identity of individuals defending territories.

Territories were identified by observing a mated pair's movements and then mapped onto a satellite image of the campground. Each territory was observed for a 2-hr time interval between 0800 and 1200 hrs CDT once a week. Nests in territories became the main focus of observations, and the identities of individuals coming and going to the nest were recorded. If a nest was not located, we followed the individuals in that territory to locate potential future nest sites. Additional observations were made if more than two individuals were found in a territory to learn if the extra birds were floaters impinging on the mated pair's territory, or if they were helpers assisting the mated pair. Helpers were classified as individuals that helped defend the territory, but did not care for the young, or as individuals observed at the nest caring for the young and defending the territory.

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RESULTS

Red-headed Woodpeckers occurred in the campground year around and at least some individuals maintained year-around territories. Eleven breeding territories were located during the 2007 breeding season. Ten territories had two individuals, while one had three individuals. Three floaters were observed in at least one census during the breeding season. Boundaries of territories overlapped with at least one other breeding territory. Two breeding pairs used utility poles as their nesting site and the other nine used trees.

There were 10 breeding territories in the 2008 breeding season. One contained three individuals while there were two each in the other nine territories. All territories in 2008 had boundaries that overlapped with at least one other breeding territory. One floater was observed during one census in the 2008 breeding season. The same two utility poles were used as nesting sites for two breeding pairs with the remainder of the breeding pairs using trees. Fifty-eight percent of the utility poles (n = 31) were used for nesting, roosting, and/or caching food.

We observed cooperative breeding in both years of study. The cooperative group in 2007 consisted of an individual with a white band and two unbanded individuals that nested in a white oak (*Quercus alba*) on the east side of the campground. All three individuals were seen simultaneously on the tree that contained the nest and responded with chatter calls when they landed near another territory member. All three also responded aggressively with nest attentiveness and alarm calls to a Red-headed Woodpecker call played in front of the tree that contained the nest. All three birds defended the territory, but only the white-banded individual and one of the unbanded individuals that had a distinctive stripe on its beak were observed tending the nest.

The cooperative breeding group during the 2008 breeding season was on the west side of the campground nesting in a utility pole. The group consisted of the same white banded individual, an unbanded bird which retained juvenile coloration around the eyes, and a third unbanded bird. All three birds defended the territory from invaders and tended the nest. All three individuals were seen on the utility pole with the nest and all flew to the utility pole when one bird emerged from the nest, giving nest attentiveness and chatter calls to one another in the process. All three were observed on several occasions taking turns incubating eggs or brooding young. All three responded aggressively with alarm calls when a Red-headed Woodpecker call was played near the utility pole.

DISCUSSION

The Red-headed Woodpecker population we studied in west-central Illinois appeared to occasionally have cooperative breeding. One breeding territory in 2007 had three individuals, all of which defended the territory, but only two were observed tending the nest. It is possible the third bird also tended the nest unobserved. One breeding territory in 2008 contained three birds, all of which defended the territory and all three were observed tending the nest. The relationship between helpers and the breeding pair was unknown because we were unable to band all birds and did not document genetic relationships. The presence of the after hatching year bird in 2008 suggests it could have been one of "white's" young from 2007. It is unclear whether these were two distinct cases of cooperative breeding or whether it was the same white-banded bird and its mate with a different helper in both years because all of the birds were not banded. This also may be an example of irregular cooperative breeding (Ligon and Burt 2004), although the breeding behavior of these birds requires further study.

The cooperative breeding we observed in addition to Short's (1982) observations of three adult Red-headed Woodpeckers tending a nest suggests a low level of cooperative breeding occurs within this species. What factors are driving cooperative breeding in our population?

First, most birds in our population maintained year-around territories which can result in greater adult survival and increased population densities, and more breeding adults than territories (Arnold and Owens 1999). Second, the open oak habitat in the park appears ideal for Red-headed Woodpeckers (Smith et al. 2000). The Red-headed Woodpecker population density in the park was greater than average for Illinois. The average number of breeding individuals in similar habitats in Illinois was 0.68/ha (Graber et al. 1977), but at our site there was an average of 1.6 breeding individuals/ha. The park is typical of many midwestern parks and campgrounds in that it is relatively open and dominated by oaks and

hickories (pers. obs.). Parks within 16 km of our site were similar structurally, but have typical numbers of Red-headed Woodpeckers (unpubl. data). The most obvious feature that distinguished our site was the large number of utility poles, the majority of which were used by woodpeckers. It is possible the utility poles make this habitat productive by providing additional nesting and food storage sites.

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Observations on the Breeding Biology of the Collared Crescentchest (*Melanopareia torquata*)

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ABSTRACT.—The Collared Crescentehest (*Melanopareia torquata*) is an endemie bird of the Cerrado (Family: Melanopareiidae), and is listed in the State of São Paulo, Brazil as "endangered". We studied the breeding biology of Collared Crescentehest at two nests in the State of São Paulo, southeast Brazil. Males were identified genetieally and equipped with radio-transmitters. The ineubation period was 12–16 days and the nestling period was 12–14 days. Nestling body mass was measured every seeond day for the first 10 days. Males partieipated in incubation and helped with nesting eare. Measurements of eggs and nests are compared to those from the single previously knòwn nest. These data are the first for any member of the Family Melanopareiidae. *Received 27 March 2009. Accepted 28 August 2009.*

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Little is known about the life history and ecology of tropical species, particularly with regard to endangered and threatened species of the Melanopareiidae and Rhinocryptidae (Krabbe and Schulenberg 2003). Recently, the nest, eggs,

and young of the Collared Crescentchest (*Melanopareia torquata*) were first described (Gressler and Marini 2007). The Collared Crescentchest is an endemic bird of the Cerrado region (Silva and Bates 2002). Willis and Oniki (2003) indicated the population is declining in the State of São Paulo, Brazil. The species is classified as "Endangered" in the List of Animals Threatened with Extinction in the State of São Paulo (Decree 53.494, 2 Oct 2008).

Conservation of biodiversity requires a refined knowledge of species and their biology, especially in the tropics, where life histories of birds have been little investigated (Stutchbury and Morton 2001). Our study was directed at adding new natural history information about the Collared Crescentchest, especially reproductive and behavioral aspects with a conservation focus. We asked the following questions: (1) are both parents involved with incubation and nestling care, (2) what is the nest visitation frequency of adults, and (3) how long do nestlings stay in the nest?

METHODS

Study Area.—This study was conducted in the 2,300-ha Estação Ecológica de Itirapina (EEI) in the municipalities of Itirapina and Brotas (22° 15′ S, 47° 49′ W) in São Paulo State, Brazil. This area is one of the last remnants of natural grasslands and grassland savannahs in São Paulo State (Gianotti 1988). The Cerrado has a complex of physiognomies from open grasslands (campo limpo) to forest (cerradão), including intermediate types "campo sujo", "campo cerrado", and "cerrado *sensu stricto*" (Ribeiro and Walter 1998). Climate in this region, according to Köppen's (1948) classification, is defined as Cwa type, receiving on average 1,376 mm of precipitation annually. During the dry season (Apr–Sep), rainfall ranges from 32 to 88 mm per month and, during the rainy season (Oct–Mar), from 117 to 257 mm per month (DAEE Post D4-014, Itirapina, SP).

Field Procedures.—We captured individual Collared Crescentchest, after hearing them, using a single mist net (12 × 2 m) and, at times using playback calls. Males and females were identified genetically by taking blood samples (0.1 ml) from the jugular vein with analysis at the Laboratório de genética e evolução de aves in the Universidade dc São Paulo following Griffiths et al. (1998).

We attached LD-2 radio transmitters (Holohil Systems Ltd, Carp, ON, Canada) using a backpack harness on 10 individuals. We obtained radio-telemetry data between October and November 2007 during the morning (0600–1200 hrs) and evening (1600–1800 hrs) in areas of "campo sujo" and "campo cerrado". We located nests by following these individuals and observing their behavior. Nests were monitored every 2 days and the behavior of parents was observed during each visit for 30 min at a distance of ~ 15 m from the nest. Observations were conducted 3 hrs after sunrise, 3 hrs around noon, and 3 hrs before sunset. This procedure allowed us to record frequency and duration of visits to the nest. We measured body mass using a spring scale (Pesola, 50 g, accurate to 1 g), and size of eggs and nestlings was measured with a digital calliper (Mitutoyo, 0.01 mm precision).

RESULTS

We found two nests of *M. torquata* in 2007. Both were woven of dry grass leaves and a few dry leaves of trees or shrubs. One of the nests was half covered by grass leaves of *Loudetiopsis chrysothrix* (Poaceae), a grass commonly observed in the area.

Average egg mass was 1.55 g, and average egg width and length was 19.05 and 14.95 mm, respectively (Table 1). Eggs were ovoid-shaped, unspotted with a greenish-blue coloration. The incubation period was 12–16 days. The first nest, with two nestlings, was found in an area of "campo sujo" on 12 November. Both nestlings left the nest 12 days later on 24 November. Considering developmental stage of the nestlings at the moment of nest discovery, the birds probably fledged 13–14 days after the eggs hatched. The second nest, with two eggs, was found on 19 November in an area of "campo cerrado". One egg hatched on 29 November and the offspring fledged 12 days later. However, this nestling may have fledged 1–2 days prematurely due to our visits. We could still detect the parents around the nest 2 days after the young fledged, where they gave a "pirrr" call. The other egg did not hatch and was collected (deposited in the Museu de Zoologia da Universidade de São Paulo). The growth rates of three nestlings were similar (Fig. 1).

Both males and females shared incubation and nestling care. The male made few visits to the nest, which were brief (1–2 min) and without periodicity. We recorded two visits during the nestling period in midday and one during

TABLE 1. Measurements of three nests of the Collared Crescentchest obtained by Gressler and Marini (2007) in Distrito Federal and average measurements of two nests during the present study, in São Paulo, Brazil.

Characteristics	Gressler and Marini (2007)	Present study
Width of entry, cm	4.2	6.0
Height of entry, cm	3.7	5.25
Nest length, cm	10	14.75
Nest depth, cm	10.5	14.75
Height from nest's base to the ground, cm	13.5	15.5
Egg mass, g		1.55
Egg width, mm	21.2/19.5	19.05
Egg length, mm	15.7/15.4	14.95
Incubation period, days	15–18	12–16
Nestling period, days		12–14

afternoon. A male was in the nest during incubation twice in the morning. It is probable the males knew of our presence during monitoring, which may have affected their behavior.

DISCUSSION

The proportions of the two Collared Crescentchest nests we found were similar, but larger (Table 1) than those of the nests described by Gressler and Marini (2007). They also observed that dry leaves in the nests were used only as support. Egg color was similar to that described by Gressler and Marini (2007), but differed from the descriptions of Sick (1997) for coloration of Olive-crowned Crescentchest (*Melanopareia maximiliani*) eggs by the lack of any speckles. Eggs in this species were whitish with large dark gray speckles near the large end (Di Giacomo 2005).

Periodicity of nest visits was low, which may reflect a strategy against predators, thus reducing chances of discovery of nests and eggs or nestlings (Skutch 1976). We also noted a different "pirr" call from adults near nests and suggest that one of the functions of this call is to keep the young near the nest, a behavior that may increase their survival (Martin 1996, Stutchbury and Morton 2001).

Our study complements the known life history information of the Collared Crescentchest, a species less studied, and contributes to the knowledge of the behavior and reproductive ecology of tropical birds.

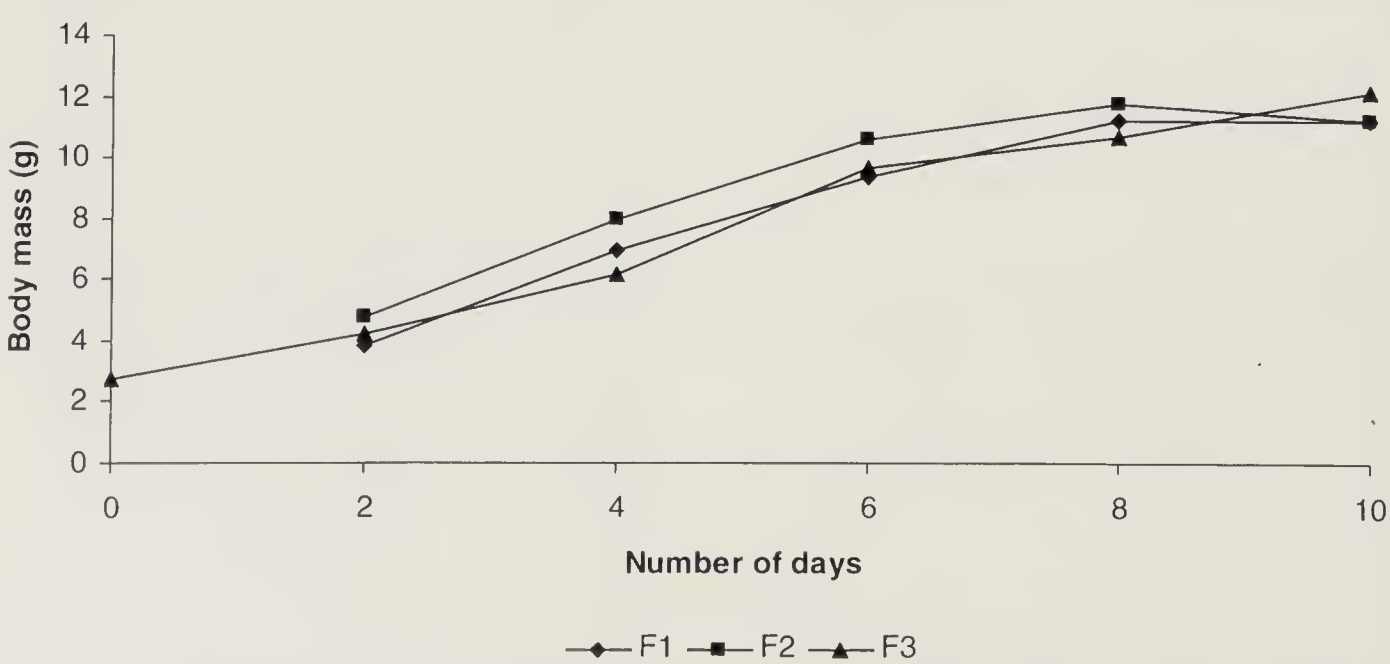

FIG. 1. Growth rates (body mass) of three (F1, F2, F3) Collared Crescentchest nestlings measured every 2 days. F1 and F2 (Nest 1) were monitored between 12 and 24 November 2007. F3 (Nest 2) was monitored from hatching on 29 November to 11 December 2007.

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Effects of a Flood on Foraging Ecology and Population Dynamics of Swainson's Warblers

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ABSTRACT.—Swainson's Warblers (*Limnothlypis swainsonii*) have been described as terrestrial leaf litter foraging specialists, and are thought to vacate flooded areas entirely. We report Swainson's Warblers occupying a flooded area in Arkansas and foraging on unusual substrates. We observed Swainson's Warblers feeding in novel ways in the tree canopy and on floating debris. This is the first report of Swainson's Warblers occupying and foraging in flooded habitat, and suggests this species may have more short-term flexibility in foraging substrate than previously thought. Return rates to flooded territories were reduced compared to years without floods and several marked individuals switched to an unflooded area protected by man-made levees. The altered hydrology of rivers constrained by levees may reduce habitat quality for this species. *Received 19 February 2009. Accepted 14 September 2009.*

The Swainson's Warbler (*Limnothlypis swainsonii*: Parulidae) is a medium-sized wood-warbler that breeds in the southeastern United States, winters in the Caribbean Basin, and inhabits areas with dense understory vegetation (Brown and Dickson 1994). Pairs are socially monogamous,

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and males exhibit breeding site fidelity and defend their territory against conspecific males (Brown and Dickson 1994). Swainson's Warblers are uncommon and local throughout their breeding range, and are ranked among the highest-priority species for conservation (Partners in Flight 2007).

Swainson's Warblers forage for arthropods in terrestrial dead leaf litter, primarily by flipping dead leaves and poking their beaks into litter on the ground (Meanley 1970, 1971; Barrow 1990; Graves 1998). Barrow (1990) classified 82% of foraging substrates (n = 41) as dead leaves, ground litter, or fallen debris, and classified the remainder as live leaves or herbs. Most (99%) observations of foraging Swainson's Warblers (n = 399) by Graves (1998) involved lifting dead leaves from the ground. More rarely, they have been reported feeding at shrub level and hawking insects (Meanley 1970, 1971; Barrow 1990), although Graves (1998) attributed arboreal foraging observations to instances of birds disturbed by humans or audio playback. Swainson's Warblers at times sing from branches in the mid-story (Meanley 1968), but they are considered primarily ground foragers (Brown and Dickson 1994, Graves 1998).

Meanley (1966) reported that none of four territorial males returned to an area they had used the previous year after a spring flood in Georgia, and characterized the effect of flooding on Swainson's Warblers as "devastating." Benson and Bednarz (2010) examined Swainson's Warbler habitat in Arkansas several years after flooding and found only nine of 42 previously occupied locations were still occupied by Swainson's Warblers. Graves (2001) and Klaus (2004) also reported abandonment of flooded territories. It is not unusual for Swainson's Warblers to occur adjacent to water or to inhabit areas that can be seasonally flooded, but flooding during the breeding season is thought to preclude site occupancy (Graves 2001, Brown et al. 2009).

Our objective is to report on response of Swainson's Warblers to a catastrophic flood event. We hypothesized that flooding would make the leaf litter and other ground debris unavailable for foraging, and therefore cause individuals to vacate an inundated area, possibly even resulting in local population extirpation.

OBSERVATIONS

Our observations were made in the Alligator Lake area of White River National Wildlife Refuge (WRNWR), Arkansas (34° 2′ N, 91° 5′ W) from 24 April to 6 May 2008. This site was being studied as part of an ongoing project: (1) it had a continuous Swainson's Warbler population since at least 2000, (2) had been intensively studied since 2004, and (3) most territorial males were color-banded. The site is several meters higher in elevation than most of the refuge, which protects it from flooding in most years allowing development of dense understory vegetation preferred by Swainson's Warblers. Heavy rains in spring 2008 caused the White River to rise, flooding WRNWR, which is within earthen levees that contain the river. The floodwaters that would have naturally inundated the much larger floodplain were confined within the boundaries of the levees. High water in the Mississippi River also prevented normal drainage of the White River. Additionally, an Army Corps of Engineers pumping plant was pumping water into WRNWR from agricultural areas bordering the refuge. The site became completely inundated in late March and the water started to recede in late April, disappearing (except for isolated pools) by 6 May 2008.

The first Swainson's Warblers returned to this site on 8 or 9 April in 2005 through 2007 (years with no flooding). We surveyed all previously known Swainson's Warbler territories in the study area beginning 24 April 2008 via canoe by listening for their songs and using audio playbacks. We encountered Swainson's Warblers singing and foraging in trees in areas that were inundated with 0.91–2.75 m of water.

We observed four Swainson's Warblers foraging in atypical ways. One unbanded male *sally-hovered* (terminology follows Remsen and Robinson 1990) above a pile of floating debris and appeared to attempt to pick an insect from it. This bird then perched on a vine (*Smilax* spp.) 2 cm above the water and picked an insect from the flotsam. A banded male was observed hopping along horizontal branches of a tree ~ 10 m above the water level, using typical leaf-lifting motions to search for arthropods under loose pieces of bark. This bird methodically hopped along one horizontal branch, looking for arthropods under loose bark, then *gleaned* insects from several other large horizontal branches, until it flew to the canopy of another tree. We observed a different banded male and one banded female on separate occasions searching for insects by lifting leaves from hanging dead leaf clusters lodged in tree

limbs. We observed some of these activities after we had judiciously used audio playback, and in other instances, we had not used playback.

We observed 10 different males and four females in flooded habitat, including four instances of pairs traveling together. Seven of the 10 males were banded and three were unbanded. One male that settled in flooded habitat had been banded at WRNWR as a nestling in 2007 (T. J. Benson and NMA, unpubl. data). We detected one male in 2006 and 2007 holding a territory outside the levee bordering the refuge. This area remained dry during the flood, and the number of males detected holding territories outside the levee increased to six in 2008, including four color-banded males that held territories inside the levee in previous years.

DISCUSSION

Some Swainson's Warblers survived the period of flooding and eventually settled on territories when the water receded, but we found reduced return rates of color-banded individuals and reduced site occupancy in 2008. We detected 25 males in 2008, compared to higher numbers in previous years (40 in 2005; 43 in 2006; 47 in 2007; Benson 2008, Anich et al. 2009). The return rate for color-banded males from 2007 to 2008 was 0.36 (17 of 47), compared to higher proportions in previous years (0.53 from 2005 to 2006; 0.58 from 2006 to 2007; Benson 2008, Anich et al. 2009).

These are the first observations of Swainson's Warblers foraging in the tree canopy. Tree branches and floating debris were the only substrate available on which birds could feed during the prolonged flooding period. We observed birds using previously unreported foraging substrates, but these birds were using typical foraging maneuvers supporting Graves' (1998) observation that Swainson's Warblers use a limited repertoire of foraging maneuvers. Graves (1998) classified 99% (n = 399) of foraging maneuvers as "leaf lifting," which occurred with associated *gleaning*, *probing*, and *gaping* motions, and two instances of *flush-pursuit* of moths (Lepidoptera) from the leaf litter. Strong (2000) found 80% of foraging maneuvers in wintering areas consisted of leaf lifting. Barrow (1990) reported that 63% of foraging maneuvers (n = 41) were *flaking* (analogous to leaf lifting), 32% *gleaning*, and 5% (2 instances) sally-gleaning (includes *sally-strike* and *sally-hover*; Remsen and Robinson 1990).

The literature, to our knowledge, does not report Swainson's Warblers occupying flooded landscapes or feeding above shrub-level height. Thus, we were surprised to document their return to breeding areas during the flood and their use of novel foraging substrates. It is perhaps not surprising that Swainson's Warblers have evolved the flexibility to survive temporary flooding, as they often inhabit bottomland forests. However, anthropogenic changes to natural flooding regimes appear to have increased the duration and depth of the high water at our site, and at other sites occupied by Swainson's Warblers (Graves 2001, Thompson 2005). Some Swainson's Warblers persisted at the site through the flood and settled on territories when the flooding subsided. However, lower return rates of color-banded individuals and reduced site occupancy in 2008 suggest that other individuals either vacated their territories when confronted with flooding or perished.

Several authors have noted abandonment of territories after flooding (Meanley 1966, Graves 2001, Klaus 2004). Previously we assumed the mechanism by which flooding prevented Swainson's Warbler occupancy was through direct removal of the primary foraging substrate. Our observations suggest that abandonment may result from the initial effects of the flood (i.e., elimination of ground for foraging) but also longer-term changes that reduce habitat quality for Swainson's Warblers. Benson and Bednarz (2010) examined Swainson's Warbler habitat at WRNWR and three other sites within 3 years of flooding and found only 21% of sites occupied after the flood. They also found that locations exhibiting more flood-related habitat changes, such as reduced leaf litter and shrub cover, were more likely to be unoccupied. We observed that Swainson's Warblers have the flexibility to survive short-term flooding, but flooded and recently flooded habitats appear to be suboptimal for this species.

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Predator Vocalizations Affect Foraging Trade-offs of Northern Cardinals

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ABSTRACT.—We investigated the roles of food quality and predator avoidance in shaping foraging behavior of Northern Cardinals (*Cardinalis cardinalis*). Cardinals visited feeders near cover and feeders with sunflower seed significantly more than they visited those in the open and those with commercial wild bird seed mix. Cardinals with a choice between their preferred food and preferred location visited the sunflower seed feeder in the open significantly more than the mixed seed feeder near cover, despite their prior preference for feeding near cover. We recorded visits to these feeders over a 2-day period during which we played Cooper's Hawk (*Accipiter cooperi*) calls every 2 hrs. The overall visitation rate did not decrease significantly, nor did the visitation rate to feeders near cover increase significantly. However, the decrease in the visitation rate to feeders in the open approached significance. Overall, we observed a significant shift in the proportion of visits to feeders near cover (containing less preferred seed). We conclude Northern Cardinals are sensitive to both food quality and predation risk, and adjust foraging to prevailing perceptions of risk. *Received 23 March 2009. Accepted 23 July 2009.*

Natural selection should favor organisms that make optimal foraging decisions when presented with conflicting options (Lima and Dill 1990, Krebs and Kacelnik 1991, Cuthill and Houston 1997). The efficiency of energy/nutrient intake and avoidance of predation are particularly important factors affecting foraging animals (Dill and Fraser 1984, Lima 1985, Lima and Valone 1986, Valone and Lima 1987). Many passerines prefer to feed near cover due to higher risk of predation in the open by *Accipiter* hawks (Morse 1973, Barnard 1979). Feeding in open areas increases a bird's visibility and the time it takes to reach safety (Pulliam and Mills 1977); small birds spend less time scanning for predators when

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near cover (Caraco et al. 1980). Given a particular probability of the arrival of a predator, birds should be able to perceive the relative danger of visiting feeders that differ in distance to cover (Lima 1985). Granivorous birds present an excellent system for investigating trade-offs. Not only can the quality of presented food be both quantified and controlled, but researchers can also manipulate predation risk by varying the distance to the nearest cover.

Predation risk may vary seasonally or even daily (Fenn and Macdonald 1995, Lucas et al. 1996, Lima and Bednikoff 1999). Moreover, prey species can use visual, auditory, and/or chemical cues to recognize the presence and threat level of predators (Lima and Dill 1990, McLean and Rhodes 1991). Consequently, researchers have used a variety of techniques to manipulate the perception of predation risk (Blumstein et al. 2008, Schmidt et al. 2008), including model predators (Lima 1985), playbacks of conspecific and heterospecific alarm calls (Peake 2005), and recordings of predator sounds (McLean and Rhodes 1991).

Our objectives were to: (1) assess how Northern Cardinals (*Cardinalis cardinalis*), a common feeder visitor, respond to variation in food quality and distance to cover when subject to predation by both migrant and resident Cooper's Hawks (*Accipiter cooperi*), and (2) examine if playing calls of a Cooper's Hawk near our test site would alter the foraging decisions of Northern Cardinals.

METHODS

Field Procedures.—We installed four squirrel (*Sciurus* spp.)-proof, hopper-style feeders in a semi-secluded location on the campus of Davidson College in Davidson, North Carolina, USA. Birds were acclimated to these feeders for 1 month prior to the beginning of the experiment. Two feeders were positioned 1.5 m apart, 15 m from cover, in the middle of a rectangular clearing. The other two feeders were also 1.5 m apart, and placed at the edge of the clearing 1.5 m from dense vegetation.

Northern Cardinals were by far the most common visitor to these feeders. Their large body size and aggressive behavior also minimized the potentially confounding effects of interspecific competition (Alatalo et al. 1987). The extent to which *Accipiter* hawks concentrate their hunting efforts near bird feeders is disputed (Roth and Lima 2007), but Cooper's Hawks are present in Davidson year-round and have been observed hunting at our feeders.

In our first experiment, adapted from Mumme (2003), we filled one feeder in each pair with black-oil sunflower seed and the other with ACE® brand wild bird seed mix (consisting primarily of millet, but also with milo and black-oil sunflower seed). We allowed birds several days to acclimate to the feeder contents before beginning observations. We recorded the number of feeding visits by cardinals at each feeder for four 1-hr observation periods per day. Observations were made from a chair ~ 50 m from the feeders. All observations occurred between 1000 and 1800 hrs EDT. A feeding visit was one in which the bird was observed to land and consume at least one food item. We did not quantify the amount of food consumed or the length of each feeding visit. Cardinals were not individually marked and it is probable that we re-sampled many of the same individuals, violating strict independence. However, several factors convinced us to pursue the study. First, the nutritional state of any bird (as well as the danger associated with visiting a particular feeder) can change over the course of a day. Second, the number of cardinals in the area was large (up to 10 were observed in the vicinity of the feeders at any given time). Third, capturing and color-banding all birds present prior to conducting this undergraduate experiment was not feasible.

We recorded feeding visits on 12 and 13 September 2007. We switched the food type in each feeder pair at 1800 hrs on 13 September to control for any locality or feeder preferences within the pair. We allowed birds to acclimate to the change in seed location on 14 September and resumed data collection on 15 and 16 September.

We again changed the contents of the feeders at 1800 hrs on 16 September, placing the favored seed type from 12 to 16 September into the two feeders in the center of the clearing and the other seed type into feeders near cover. We allowed birds to acclimate to the new locations on 17 September and resumed data collection on 18 September, continuing through 21 September. We continued to use two feeders at both locations to minimize the chance that subordinate individuals would be forced to visit undesirable feeders.

We repeated this trial on 30–31 January 2008 with preferred seed in the open and the non-preferred seed near cover. We collected data from

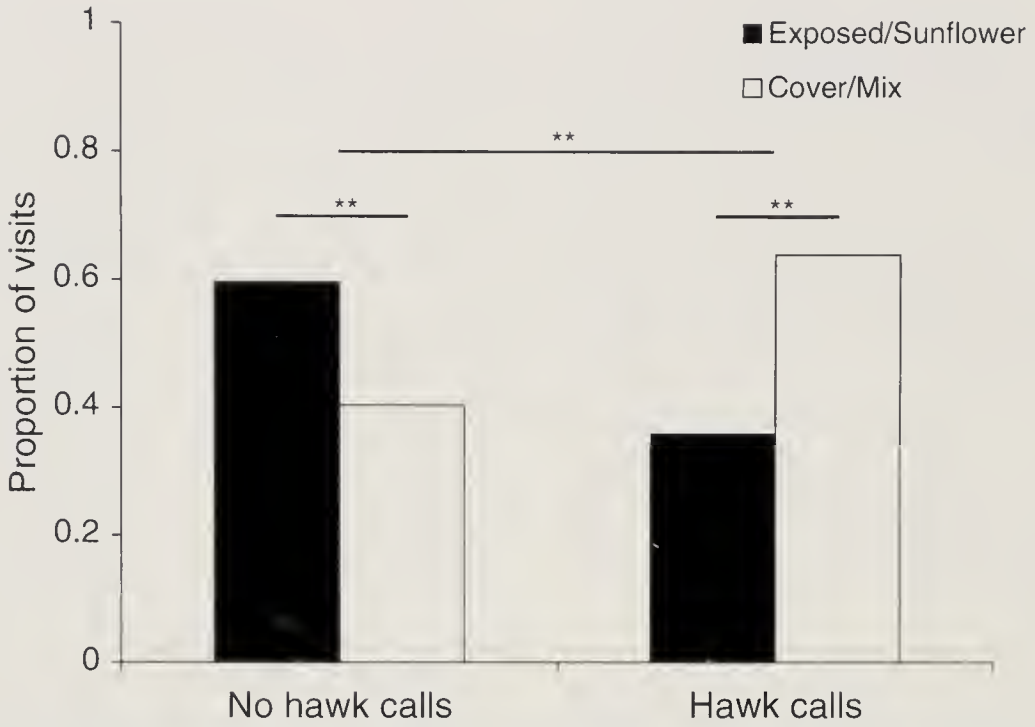

FIG. 1. Northern Cardinal visitation in winter 2008 to exposed feeders with preferred food (sunflower seed) vs. visits to less preferred food near cover on days without (n = 668 visits) and with (n = 455 visits) Cooper's Hawk call playback (** = $P < 0.001$).

this trial in three 1-hr sessions per day (1 hr between 0800 and 1100 hrs EST, another between 1100 and 1400 hrs EST, and again between 1400 and 1700 hrs EST). We played calls of a Cooper's Hawk (Neville 2004) on 1 and 2 February at 0800, 1000, 1200, 1400, and 1600 hrs. We recorded feeder visits by cardinals on these days as we had on 30–31 January. Playbacks consisted of a 5-sec call played 12 times in succession. Calls were played at a natural volume from a hidden position 80 m from the feeders. We did not have an explicit control playback because of the indirect nature of the hawk playback and the richness of the acoustic environment (corvids, dogs, car horns, trucks).

Statistical Analyses.—We used JMP 7.0 (SAS 2007) to analyze our data. We performed X^2 tests to compare relative use of feeders containing different seeds, feeders in different locations, and feeders in the presence and absence of Cooper's Hawk calls. We used Wilcoxon/Kruskal-Wallis tests to assess absolute changes in feeder visitation rates resulting from playback of hawk calls. Data are presented as means ± SE.

RESULTS

Northern Cardinals visited feeders containing sunflower seed significantly more often than those with mixed seed (X^2_1 = 22.2, $P < 0.001$) when both foods were provided at both locations. Sixty-four percent of 532 visits were to feeders containing sunflower seeds. Cardinals visited feeders near cover significantly more often than those far from cover (X^2_1 = 36.6, $P < 0.001$). Sixty-eight percent of 532 visits were to feeders near cover.

We provided cardinals with a choice between their preferred food type (sunflower seed) and preferred location (near cover) in the next phase of the experiment. Cardinals visited the exposed sunflower seed significantly more often than mixed seed near cover (X^2_1 = 34.3, $P < 0.001$). Sixty-seven percent of 571 visits were to the exposed feeders containing sunflower seed.

We repeated the trial to ensure the cardinals continued to prefer higher quality seed in a less safe location, even in winter. Cardinals visited the exposed feeders significantly more often (X^2_1 = 12.4, $P < 0.001$), as we found in the fall. Sixty percent of 668 visits were to the exposed feeders containing sunflower seed (Fig. 1). We then moved on to our playback experiment. The decrease in the mean visitation rate of cardinals as a result of exposure to hawk calls (47.7 ± 8.6/hr to 37.8 ± 4.9/hr) was not significant (Wilcoxon/Kruskal-Wallis Z = −0.54, P = 0.59). The increase in use of feeders near cover (38.6 ± 5.3/hr to 48.3 ± 5.3/hr) was not significant (Wilcoxon/Kruskal-Wallis Z = −1.14, P = 0.25), but the decrease in the visitation rate to exposed

feeders (56.9 ± 16.3/hr to 27.3 ± 5.6/hr) approached significance (Wilcoxon/Kruskal-Wallis $Z = -1.79$, $P = 0.074$). Overall, exposure to Cooper's Hawk calls resulted in a dramatic and significant shift in feeder use ($X^2_1 = 60.0$, $P < 0.001$; Fig. 1). Cardinals, instead of preferring the higher quality seed in the exposed location, as they had in the first 2 days, had a significant preference for the lower quality seed in the safer location on playback days ($X^2_1 = 18.1$, $P < 0.001$). Only 36% of 454 visits were to exposed feeders containing sunflower seed (Fig. 1).

DISCUSSION

A basic tenet of foraging theory is that organisms seek to maximize energy acquisition (Krebs and Kacelnik 1991, Cuthill and Houston 1997). One means by which this can be achieved is by foraging selectively, concentrating on higher quality foods when opportunities present themselves. We presented cardinals with black-oil sunflower seeds (with shells) versus commercial wild bird seed mix in our experiment. We were not surprised that, when presented with both foods at both locations, cardinals visited feeders with sunflower seed significantly more often; relative to commercial wild bird seed, black-oil sunflower seed has a high energetic content and nutritional value (Willson 1971, Willson and Harmeson 1973). It is possible that cardinals varied the length of their stay (and quantity of seed ingested) at feeders, but our results suggest that visitation rates alone provide a meaningful comparison.

Foraging organisms are also under pressure to minimize risk of death from predation (Lima and Dill 1990, Lima 1998). Cardinals should be sensitive to risks associated with different feeding locations and, all things being equal, should spend more time in safer foraging locations (those near cover) and less time in dangerous locations (those in the open). We were not surprised to find that, when presented with both foods at both locations, cardinals visited feeders near cover significantly more often.

Optimizing foraging requires making decisions when all things are not equal (Sih 1980, Lima and Dill 1990, Cuthill and Houston 1997). In the first trial, the strength of the preference for sunflower seed was ostensibly similar to the preference for foraging near cover. However, when cardinals had to choose between their preferred food and their preferred location, they showed a clear bias toward higher quality food (sunflower seed)—even though it was available only in the dangerous (exposed) location. This suggests that cardinals can recognize a risk of feeding in exposed locations, but willingly incur that risk to obtain high quality food.

Our last experiment demonstrated the cardinals we observed were not applying a single assessment of risk to foraging activities. Most cardinals under normal conditions perceived a threat in foraging at the exposed feeders, but not sufficiently great to forego sunflower seeds when available only at exposed feeders. However, upon hearing hawk calls in the vicinity throughout the day, cardinals adjusted their perception of risk. Neither the decline in the visitation rate to all feeders nor the increase in the visitation rate to feeders near cover was significant, but the decline in the visitation rate to exposed feeders approached significance. We observed a significant change in the relative use of exposed and protected feeders. Most cardinals were unwilling to risk predation to obtain higher quality food when exposed to the calls of a Cooper's Hawk. Our experiment lacked an explicit control playback, but the strength of the foraging response suggests the trends we observed were real. This plasticity is presumably adaptive, allowing individuals to maximize their fitness (Lima and Bednikoff 1999).

Birds recognize, assess, and respond to danger using a variety of cues including visual, auditory, and even olfactory (Roth et al. 2008). The cardinals we tested altered their foraging strategy dramatically to the playback of hawk calls, but these results are not always obtained. Schmidt et al. (2008) observed that eastern chipmunks (*Tamias striatus*) altered their foraging in response to the alarm calls of Tufted Titmice (*Baeolophus bicolor*), but not to the calls of an actual predator, the Broad-winged Hawk (*Buteo platypterus*). Schmidt et al. (2008) hypothesized the hawk call provided information upon which chipmunks could make a foraging decision, whereas the titmouse call simply alerted them to an eminent danger for which additional vigilance and information would be required. Similarly, Van der Veen (2002) found that Yellowhammers (*Emberiza citronella*) exposed to an accipter model resumed foraging sooner than individuals with less reliable information (those which did not see the model but did hear the alarm calls of those exposed to the model). Our experiment is the first to demonstrate that Northern Cardinals weigh the

importance of food quality differently in response to auditory cues of the presence of a particularly dangerous predator.

The plasticity we observed suggests the outcomes obtained were particular to the circumstances of our experiments. Our results may have been different had we varied certain aspects of our design (e.g., types of food used in the feeders). Moreover, had our exposed feeders been placed in a large field 50 m from the forest edge, rather than in the center of a small meadow, the perceived risk involved in visiting them may have differed. Our findings suggest that Northern Cardinals in our population tended to respond in an adaptive way to variation in food quality and differing levels of predation risk.

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Observations and Predation of a Coral-billed Ground Cuckoo (*Carpococcyx renauldi*) Nest in Northeastern Thailand

Korakoch Pobprasert[1] and Andrew J. Pierce[1,2]

ABSTRACT.—We found the first documented wild nest of a Coral-billed Ground Cuckoo (*Carpococcyx renauldi*) at Khao Yai National Park, Thailand in June 2007. The large stick nest was monitored for 24 days including 1095 hrs of video footage; it contained two eggs and was in dense vegetation 4.85 m above the ground. Nest attentiveness of adults was almost constant with both birds taking turns to incubate or brood. Food delivered to nestlings included lizards, nestlings, a snake, frogs, earthworms, and other invertebrates. Nest defense was observed against several known nest predators but the nest ultimately failed due to predation by a pig-tailed macaque (*Macaca nemistrina*). These observations provide insight into the breeding ecology of the only two congeners, *C. viridis* and *C. radiceus*, for which little is known of their ecology and both are endangered. *Received 27 March 2009. Accepted 18 September 2009.*

There is an extreme paucity of studies on the breeding ecology of tropical Asian birds (Sodhi and Brook 2006) and they should not be assumed to have the same life histories as the more widely studied neotropical birds. It is essential that studies are undertaken for the long-term management of bird communities as forest cover and forest quality continues to decline in Asia (FAO 2009).

There are 11 species of non-parasitic cuckoos on mainland Southeast Asia including: six malkohas (*Phaenicophaeus*), four coucals (*Centropus*), and one ground cuckoo (*Carpococcyx*). There are two other ground cuckoos which inhabit the forests of Sumatra and Borneo. The Sumatran Ground Cuckoo (*Carpococcyx viridis*) has only recently been rediscovered (Zetra et al. 2002) and nothing is known of its breeding ecology; it is Critically Endangered (IUCN 2008). The Bornean Ground Cuckoo (*C. radiceus*) is Near Threatened (IUCN 2008) and what is known of its breeding ecology is vague and ambiguous derived from a few captive birds and questionable museum specimens (Long and Collar 2002). Most widespread of the three species is the Coral-billed Ground Cuckoo (*C. renauldi*) (CBGC), that occurs in Thailand, Cambodia, Laos, and Tonkin and Annam (Vietnam). It is an uncommon resident of broad-leaved evergreen forest and secondary growth up to 1,000 m asl in Thailand (Robson 2000); its conservation status is of Least Concern (IUCN 2008). The only documented nesting attempts are of captive pairs. A pair at Metro Toronto Zoo produced 13 fledglings and clutches of up to five eggs were laid between early April and mid-August from 1976 to 1979 (Atkinson 1982). Robiller et al. (1992) and Rinke (1999) both document nests of captive pairs with clutches of 3–4 eggs and nestlings reared by hand.

We present details, obtained through video recordings, of the first documented wild nest of a Coral-billed Ground Cuckoo, including its predation by pig-tailed macaques (*Macaca nemistrina leonina*) in Khao Yai National Park, northeastern Thailand in 2007.

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METHODS

We initiated a 3-year study of nest predation in 2006 on birds in the Mo-Singto area of Khao Yai National Park (14° 26′ N, 101° 22′ E), Nakhon Nayok Province, Thailand. Small waterproof Fujiko™ cameras (65 × 65 × 85 mm) with infrared diodes for 24-hr surveillance were deployed 3–5 m from nests of ground and understory nesting birds. The cameras were attached by cables to a digital video recorder (DVR) placed 20–25 m from the nest whereby the power source and DVR could be changed without disturbing the nesting birds (Pierce and Pobprasert 2007). A small microphone was also fitted within the surrounding case of the camera. Data from the DVR were stored on DVDs for later analysis. Cameras have been shown to have little effect on nesting success when placed off the ground (King et al. 2001, Staller et al. 2005, Pierce and Pobprasert 2007). Measurements of the nest were taken after it had failed. Male Coral-billed Ground Cuckoos are slightly larger than females, but they are monomorphic in plumage and males and females are indistinguishable in the field.

RESULTS

An adult Coral-billed Ground Cuckoo was observed to fly down from a tree within a dense tangle of woody climbers on 13 June 2007. Closer inspection on 17 June revealed a nest containing two white eggs. A camera was placed in an adjacent tree ~4 m from, and slightly below, the nest which still contained two eggs at 1400 hrs on 18 June. The sitting bird flushed quickly and silently as we approached the nest area on each of these visits despite our attempts to avoid disturbing it. An adult returned to incubate within an hour of us leaving the area after initial setting of the camera. Apart from a mechanical failure for 8 hrs on 1 day during incubation, the cameras recorded continuously until the nest was predated on the morning of 7 July. The adults were only disturbed once following placement of the camera when a person inadvertently passed close to the nest.

Nest Placement.—The nest was in seasonally wet evergreen forest at 725 m asl. The canopy was generally 20–30 m high with emergent trees up to ~60 m, but the area within 20 m of the nest included an old tree fall with most trees less than 10 m in height and covered with masses of woody climbers. The nest was an untidy pile of dead twigs in the shape of a shallow cup similar to that of a large raptor. It was lined with a few fresh small twigs that still had green leaves. It was placed at the base of a branch forking from the leaning trunk of a tree with a diameter at breast height of ~10 cm, and further supported by woody climbers. The rim of the nest was 4.85 m above ground and vegetation, in the form of small branches and woody climbers, extended 50–60 cm above the nest. The outer diameter of the nest was 33 cm, and the total height was ~25 cm.

Parental Care and Food Provisioning.—Both adults shared incubation duties and one adult was on or close to the nest at all times with few exceptions. There may have been some contact calls from the returning bird as the sitting bird became aware of the incoming bird shortly before it arrived at the nest but, if so, they were too soft to be picked up by the microphones. Both adults usually brought a small twig complete with fresh green leaves and placed it in the nest during the egg stage before commencing incubation.

The adults changed brooding only twice per day with changeover times quite variable; the first between 0921 and 1338 hrs and the second between 1612 and1754 hrs. Changeovers typically took <30 sec with two of exceptionally longer duration of 2 min 32 sec and 8 min 32 sec. Excluding these apparent anomalies, changeovers, from when the sitting bird left the nest until the other bird resumed incubation, averaged (± SD) 20 ± 11 sec (n = 24). The bird incubating during the day averaged (± SD) 5 hrs 36 ± 52 min (n = 12) on the nest while the bird that incubated overnight averaged 18 hrs 43 ± 50 min (n = 12) on the nest. We were unable to identify gender of the adults; however, for 9 days where the data are continuous, and one or both adults were in view at all times, the same adult incubated over night as on the previous night. It is likely therefore that only one male or one female incubated at night and the other during the day for the entire period. Gaps in attentiveness after the eggs hatched meant we could not ascertain the proportion of time spent brooding by each bird during the nestling stage.

The first egg hatched in the early morning of 1 July when the adult started pecking at something beneath itself and ate what was presumably eggshell (no eggshells were removed and only small fragments of eggshell were found in the nest after it had failed). The second egg hatched on the morning of 2 July when the same sequence of

events occurred. Changeovers followed the same pattern during hatching as in the incubation period and it was not until 1147 hrs on 2 July that the first food item was brought to the nest. Attentiveness at the nest continued to be almost constant throughout the nestling period although visitation rates increased to provision the nestlings. There were two visits with food on 2 July followed by 16, 24, 33, and 29 visits on the subsequent 4 days and a further seven visits in the morning of 7 July. The incoming bird during the nestling stage usually perched on the rim of the nest for a few seconds before the sitting bird stood up and left. The incoming bird would then hop into the nest and feed the nestlings before brooding them.

Nestling Diet.—Only a limited number of prey items could be positively identified. These included lizards (3), nestlings of small birds (2), frogs (2), a blind snake (*Typhlops* or *Ramphotyphlops*), Orthoptera (2), and earthworms (2). Prey was too large for the nestlings to swallow on two occasions and it was either taken away or eaten by the adult. Other prey items tentatively identified were worms, caterpillars, arthropods, and slugs or snails but many of the small food items appeared to be regurgitated or were out of view of the camera.

Nest Defense.—Variable squirrels (*Callosciurus finlaysonii*) and northern tree shrews (*Tupaia belangeri*) visited the nest nine times. The adults usually turned to face these relatively small predators with crown feathers depressed and tail raised and the intruder quickly withdrew. Two visits to the nest by small snakes (~50–100 cm long; probably *Boiga* spp.) were the only potential nocturnal nest predators, and both soon retreated rapidly after reaching the sitting bird which did not react. Pig-tailed macaques passed close by twice on the afternoon of 4 July. The adult adopted a threat posture with this no doubt more serious threat to the nest and, on these occasions, the macaques left the nest alone. A troop of macaques could be heard passing the nest at 0854 hrs on 7 July and the sitting CBGC became alert raising its body and spreading its tail. At exactly 0858 hrs it raised its crown feathers and turned to face a macaque with bill open, wings apart and tail spread over its back. This macaque dropped down quickly to the nest 17 sec later and the CGBC flushed to nearby branches. It stayed within ~1 m of the nest maintaining its threat posture and making short darting movements at the macaque. However, the macaque was not deterred and grabbed the nestlings one at a time, put them quickly into its mouth and left. The whole episode took 3 sec from when the CBGC left the nest until the macaque took the nestlings and departed. The CBGC returned to the rim of the nest; when another (smaller) macaque approached, <1 min after the first attack, it flew at the macaque causing the latter to retreat; the CBGC flew on away from the nest. Two small macaques came to investigate the nest but left on finding it empty. The CBGC returned cautiously at 0918 hrs from below the nest and stood on the nest for 6 min before leaving. A CBGC entered the nest carrying a large insect at 0957 hrs but left again after nearly 1 min. After another visit at 1014 hrs with a different insect there were no further visits by 1500 hrs the following day when the camera was removed.

DISCUSSION

Coral-billed Ground Cuckoos have been recorded nesting in captivity but ours is the first observation of a wild nest and provides more appropriate information about their nesting behavior. The CBGC is under no immediate threat but there is an almost complete lack of information on the breeding ecology of the globally threatened congeners, Sumatran and Bornean ground cuckoos, the latter of which is known to be similar to CBGC (Long and Collar 2002).

The CBGC nests at the Toronto Zoo were built by both adults and were comparable in dimensions to the nest we describe (Atkinson 1982) but, otherwise quantifying these nests is not appropriate due to necessary restrictions of captive birds. We found no fecal sacs in or near the nest after it failed and it is possible the adults ate them; Robiller et al. (1992) observed the nestlings defecated on the rim of their nest, but they were being hand fed with no adult birds present. Atkinson (1982:170) states "an incubation period of 28 days seems the normal condition". However, the data are ambiguous and could be interpreted as being anywhere between 17 to 28 days while Payne (2005) reports the eggs hatch in 18–19 days. Eggs in our nest hatched within 15 days of seeing the full clutch and was probably in the early stages of incubation when found. The clutch of two eggs is at the lower end of clutch sizes reported from captive birds. Atkinson (1982) details 10 nests with clutches of 1–5 eggs (mean 3.1, median 4). Rinke (1999) details two nests with four eggs and Robiller et al. (1992) records

two nests, each with three eggs but also states the clutch size to be 3–4 eggs.

Ground cuckoos are notoriously difficult to observe in the wild and, apart from a few observations of birds coming to food waste at restaurants adjacent to the forest (Payne 2005; AP, pers. obs.), there are few published data on CBGC diet or behavior. Delacour and Jabouille (1931) reported small birds and mammals in their diet. Based on the stomach contents of a recently dead adult, found within a kilometer of this nest in 2006, they feed on a wide range of invertebrates; the stomach included the remains of several hundred individual prey items, especially Orthoptera and Isoptera but also Coleoptera, Lepidoptera, Hymenoptera, and a Chilapoda (centipede) (John Milne, in prep.) We did not definitively record any of these but it is possible they were among the many unidentified prey items fed to the nestlings. There is no evidence that they (or Bornean Ground Cuckoos [Long and Collar 2002]) eat fruit despite the generic name *Carpococcyx* meaning fruit-cuckoo.

Nest success in tropical forests is low; ~8–30% for most species with predation being the main cause of nest failure (Martin 1995, Robinson et al. 2000). Our research using video surveillance at nests in Khao Yai National Park (Pierce and Pobprasert 2007, and unpubl. data) identified the main nest predators as pig-tailed macaques, rodents (Muridae and Sciuridae), tree-shrews (*Tupaia*), birds, and snakes. Several of these were recorded visiting the CBGC nest. We recorded similar size snakes disturbing sitting Puff-throated Bulbuls (*Alophoxius pallidus*) and trogons (*Harpactes* spp.) and, being able to take the eggs or nestlings (Pierce and Popbrasert 2007). Rinke (1999) shows a CBGC on a nest in captivity in a defense posture similar that recorded at our nest. The CBGC in our study was able to deter macaques on two occasions by adopting this stance, although ultimately unsuccessful against a large macaque. A high level of nest attentiveness has been recorded for other non-parasitic cuckoos in the region (Payne 2005), and it has been suggested this may have developed in response to high predation pressures observed in the tropics (Auer et al. 2007). The constant vigilance of the adult CBGC at their nest no doubt stopped many potential predators from taking eggs or nestlings. However, adults were highly sensitive to disturbance, flushing from the nest and not returning for an hour or more afterwards, even when we approached quietly knowing the nest location. These results highlight the potential increased predation risk caused by human disturbance of nesting birds that might otherwise be able to defend their nest.

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Diet of Chinese Grouse (*Tetrastes sewerzowi*) during Preincubation

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ABSTRACT.—The endemic Chinese Grouse (*Tetrastes sewerzowi*) inhabits subalpine coniferous forests. Little is known about its diet in the breeding season, especially while birds feed on the ground. Analysis of crop contents indicated that willow (*Salix* spp.) was the primary food of males (>98% wet weight, $n = 4$), whereas Dragon spruce (*Picea asperata*) seeds and willow were the primary foods of females (both >40% wet weight, $n = 2$). Dragon spruce seeds, invertebrates (mainly ants), and forbs were frequently consumed by females, but seldom by males, possibly to meet the nutrient constraints of egg formation. We suggest the different diets of males and females of this monogamous species may be the result of females allocating more time to searching for scarce, nutritious food, whereas males spend more time in vigilance behavior. *Received 2 April 2009. Accepted 5 September 2009.*

The Chinese Grouse (*Tetrastes sewerzowi*), endemic to the coniferous forests of Qinghai-Tibet Plateau, is one of the rarest grouse species in the world (Storch 2000) and is legally considered an endangered species in China (Zheng and Wang 1998). The small body size of Chinese Grouse (Sun et al. 2005) may reduce its ability to meet nutritional requirements when feeding on plants because gut capacity scales linearly with body mass, whereas mass-specific nutritional requirements increase with decreasing body mass (Demment and Van Soest 1985). Small body size also precludes storage of energy and nutrients in the body for egg formation (Swenson et al. 1994). Chinese Grouse have the greatest nutritional investment in clutches among tetraonids (Sun et al. 2005) and longer egg laying intervals (48 hrs) than other grouse (Sun et al. 2002). Thus, nutrient constraints possibly exist for egg formation for this species and female Chinese Grouse may rely heavily on nutritionally rich food during the prelaying and laying period to gain mass and produce eggs when food may not yet be plentiful (Nager 2006).

The diet of Chinese Grouse during the breeding season is poorly known and difficult to clarify by observation because of dense vegetation and birds not habituated to observers. We present information on the diet of this monogamous grouse from analysis of crop contents to help understand its foraging strategy to meet nutrient constraints of egg formation.

METHODS

Study Area.—Our study area was in the Lianhuashan Natural Reserve, southern Gansu Province, China (34° 57′ N, 103° 46′ E). Forests occur on north-facing, and some northeast and northwest-facing slopes at elevations of 2,600–3,200 m; only shrubs and grasses grow on south-facing slopes. The main cover types are: (1) coniferous forest dominated by Dragon spruce (*Picea asperata*) and Farges fir (*Abies fargesii*), (2) coniferous-deciduous forest, including spruce, fir, Himalayan birch (*Betula utilis*), and willow

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TABLE 1. Foods in crops of six Chinese Grouse at Lianhuashan, Gansu, China (Collection dates: Male # 1, 25 Apr; Male # 2, 9 May; Male # 3, 3 May; Male # 4, 17 May; Female # 1, 16 Apr; Female # 2, 14 May).

Food	Types of food	Portion of wet weight (%)					
		Male #1	Male #2	Male #3	Male #4	Female #1	Female #2
Invertebrates (ant, midge)[a]		0	0	0	0	3.0	9.9
Willow	Twigs, buds, catkins, leaves	100	100	98.3	100	56.0	43.3
Dragon spruce	Seeds	0	0	1.7	0	40.8	43.3
Forbs[b]	Leaves	0	0	0	0	0.2	3.5
Total wet mass, g		2.3	0.3	3.2	0.3	4.9	1.5

[a] Most invertebrates were ants (Hymenoptera: Formicidae); only one midge (Diptera) occurred in the crop of Female # 2.
[b] Included *Fragaria orientalis*, *Geum aleppicum*, and *Triosteum pinnatifidum*.

(*Salix* spp.), and (3) shrublands, including willow, sea buckthorn (*Hippophae rhamnoides*), and barberry (*Berberis* spp.). The study area has been described by Sun et al. (2003).

Field and Analysis Procedures.—We defined the preincubation period as 20 April–30 May, which represents 2 weeks before egg laying to when the last egg is laid. We obtained crops of four males and two females that died from predation or during capture while attaching radio transmitters. One female which died on 16 April was also included in our analysis. Identification of gender of grouse carcasses was based on PCR amplification of CHD genes using P2/P8 primers (Griffiths et al. 1998) and sex1/sex2 primers (Wang and Zhang 2009), or based on the presence of the black chin patch for males (Bergmann et al. 1996). Age (adult or yearling) was not assigned, as there is no known reliable method (Swenson et al. 1996). Crops were removed and contents were identified, sorted, and weighed to the nearest 0.001 g. Plants were identified to species and invertebrates were identified to Order.

We sampled 13 plots (40 × 40 cm^2) where grouse pecked and counted the surface seeds to assess their availability. Seeds from cones were collected, dried to constant weight at 50° C and homogenized to measure nitrogen (Foss Kjeltec™ 2100, Hilleroed, Denmark), lipid (Soxhlet), fiber (ANKOM 200/220 Fiber Analyzer, Fairport, NY, USA), tannin (Phosphomolybdium Tungstic Acid colorimetric method, China Entry/Exit Inspection and Quarantine Association 1999), calcium and phosphorus (AOAC 1995), ash (combustion at 550° C), and energy (PARR 1281 bomb calorimeter, Moline, IL, USA). SPSS 13.0 (SPSS Inc., Chicago, IL, USA) was used for all statistical analysis. Data are expressed as $\bar{x} \pm$ SE.

RESULTS

Willow, including catkins, leaves, twigs, and buds occurred in all crops and comprised 99.6 ± 0.4% and 49.7 ± 6.4% of the wet biomass for males ($n = 4$) and females ($n = 2$), respectively (Table 1). Dragon spruce seeds were consumed intensively by females but seldom by males (42.1 ± 1.3 vs. 0–1.7% of the wet biomass). Invertebrates (ants and midges) and forbs (strawberry [*Fragaria orientalis*], yellow avens [*Geum aleppicum*], and feverwort [*Triosteum pinnatifidum*]) ranged from 0.2 to 9.9% of the wet biomass in crops of females, but were not found in crops of males.

Farges fir seeds were not found in crops of either males or females. Compared to Dragon spruce seeds, Farges fir seeds occurred in low densities on the ground (35 ± 67 vs. 296 ± 367 seeds/m^2, paired t test, $P = 0.04$, $n = 13$), and had lower protein and ash content, and higher fiber, tannin, phosphorus, and calcium content, whereas their lipid and energy contents were similar (Fig. 1).

DISCUSSION

Willow was the primary food of male grouse (>98% of wet biomass), while Dragon spruce seeds as well as willow were the primary food of females. Females ate invertebrates and forbs, whereas males did not. These findings indicate the diet of female grouse differed from males prior to incubation. This is consistent with our observations that both males and females foraged in willows intensively at dawn and dusk, but females allocated more time than their mates to foraging on the ground during the day (60.8 vs. 15.1%) (Sun 2004).

Egg formation is a demanding process in terms of energy and nutrient requirements (Nager 2006).

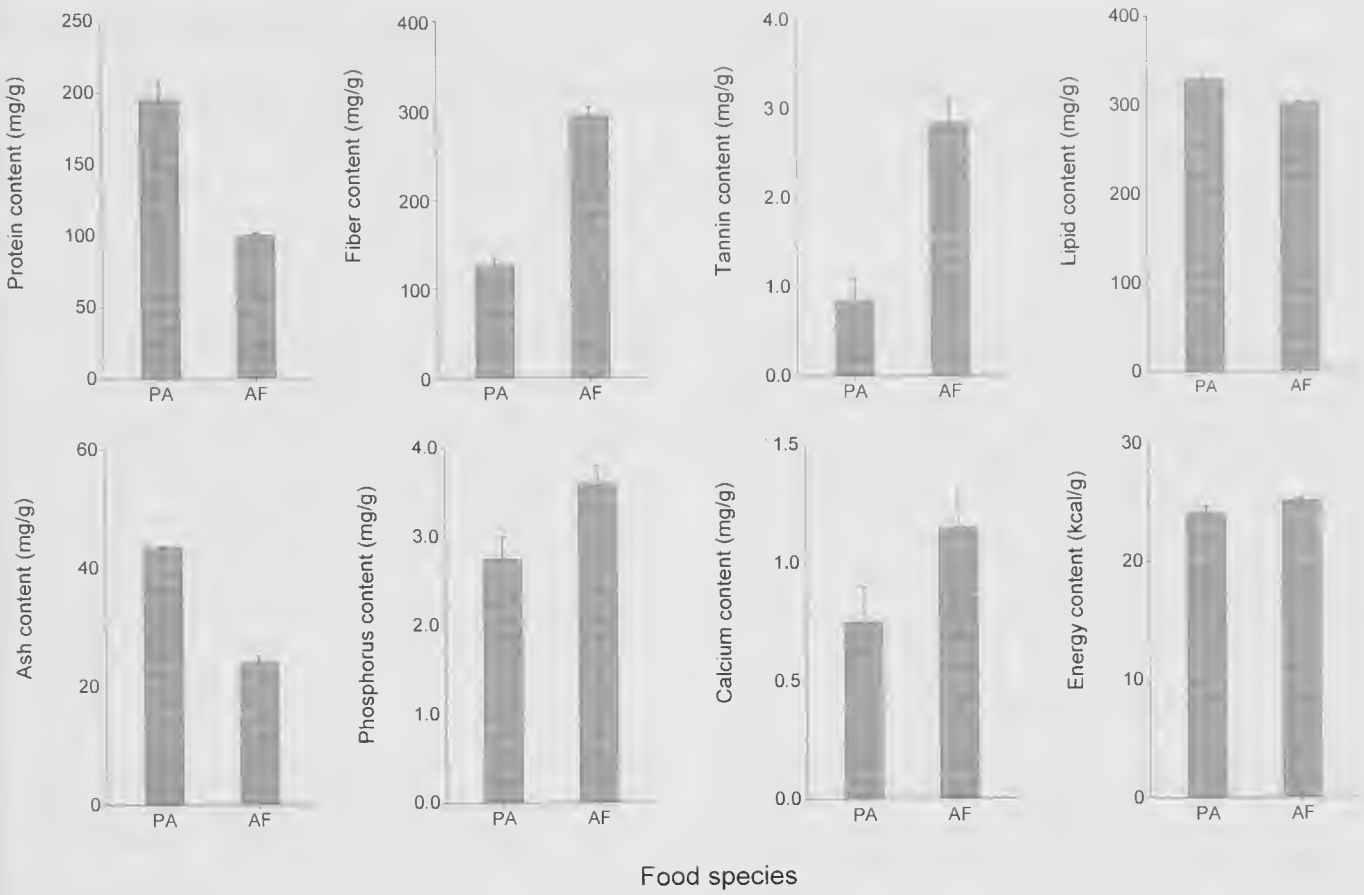

FIG. 1. Content ($\bar{x} \pm$ SE) of protein, fiber, tannin, lipid, ash, phosphorous, calcium, and energy in samples of seeds of Dragon spruce (*Picea asperata*) (PA) ($n = 3$) and Farges fir (*Abies fargesii*) (AF) ($n = 3$) collected from the ground.

Some female grouse shift dietary patterns during spring to select high-nutrient foods, including invertebrates and forbs, which are high in crude protein, calcium, and phosphorus (Swenson 1991, Barnett and Crawford 1994, Gregg et al. 2008). Female Chinese Grouse in our study similarly shifted their diet from willow to selected ground seeds, invertebrates, and forbs during the prelaying period. Female grouse in smaller species with fewer energy and nutrients reserves are more dependent on exogenous sources (i.e., nutritionally rich food) for egg production (Moss et al. 1975, Brittas 1988, Swenson et al. 1994). Green leaves typically contain lower concentrations of nutrients and are less digestible than animal tissue (Robbins 1993). Butterfield and Coulson (1975) estimated that consumption of 8% insect material in the food of Red Grouse (*Lagopus lagopus scoticus*) could increase nitrogen and phosphorus intake by 67 and 51%, respectively. Dragon spruce seeds had higher protein, energy, and lipid, and lower fiber and tannin than willow buds (unpubl. data). Thus, Dragon spruce seeds, invertebrates, and forbs may be important foods for Chinese Grouse hens during preincubation. Dragon spruce seeds rather than Farges fir seeds were consumed by hens possibly because the latter are less available on the ground and contain higher tannin and lower protein contents.

Nutritionally rich foods, including invertebrates, forbs, and Dragon spruce seeds are not highly available for prelaying hens, as it is still cold (average $<10^{\circ}$ C) and some areas are covered by snow until mid-May in the subalpine forest. These foods are less available in years of late snowmelt and could affect the breeding performance of Chinese Grouse. Clutch size was 6.2 ± 0.3 ($n = 9$) and number of chicks hatching was 2.1 ± 0.9 ($n = 11$) in a year that snowmelt was delayed by ~10 days, whereas the corresponding figures were 7.0 ± 0.3 ($n = 13$) and 5.6 ± 0.8 ($n = 13$) in a good year (unpubl. data). Our sample size was small, but we found females commonly ate nutritionally rich foods whereas males seldom foraged on them. Male Chinese Grouse in this monogamous species (Sun 2004), spend more time (60.8 vs. 15.1%) in vigilance behavior than females, allowing their mates more time to search for nutritious food.

The Chinese Grouse is listed in Category I of

nationally protected animals and for which hunting is forbidden (Sun 2000). The crop samples and diet analysis reported here are valuable and add to the knowledge of foods used by Chinese Grouse. This information is also helpful in understanding the social behavior of small monogamous birds.

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Observations of a Possible Foraging Tool used by Common Ravens

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ABSTRACT.—Common Ravens (*Corvus corax*) are opportunistic generalist foragers. Ravens during winter, in some portions of their range, rely heavily on meat scavenged from carcasses. Ravens use a variety of strategies to find carcasses on the landscape, including keying on audible cues that suggest the presence of a food source. I documented Common Ravens investigating a simulated animal distress call on 13 of 17 trials, suggesting that investigating animal distress vocalizations may be one tool in the suite of foraging strategies used by ravens. *Received 6 June 2009. Accepted 6 September 2009.*

The Common Raven (*Corvus corax*) is an opportunistic generalist forager and uses a variety of food sources including carrion, rodents, insects, nestlings, eggs, seeds, fruit, and garbage (Bent 1946, Heinrich 1988, Engel and Young 1989, Kelly et al. 2005). Many ravens at northern latitudes rely heavily on meat from carcasses of ungulates during winter (Temple 1974, Heinrich 1988, Hayes et al. 2000, Vustich et al. 2004). These carcasses are an unpredictable food source that is often difficult to locate on the landscape (Heinrich 1988, Stahler et al. 2002, Vustich et al. 2004). Stahler et al. (2002) summarized strategies that carrion feeders, such as ravens, use when foraging for carcasses as: flying the landscape and finding them visually by chance, foraging where conspecifics or other species are seen foraging, responding to vocalizations from other carcass feeders, following other ravens that have previously located food from nocturnal roost sites, and associating with predators that make carcasses available. White (2005) found that ravens were attracted to gunshots as a strategy for finding ungulate gut piles discarded by successful hunters. Ravens also cue in on appeasement calls of conspecifics (Heinrich et al. 1993) and likely the howling of wolves (Harrington 1978) as a means of finding food. These examples indicate ravens respond to audible stimuli as a foraging strategy. I present observations made during winter of ravens responding to imitation prey distress calls and suggest this response is another tool in the suite of foraging strategies used by ravens.

OBSERVATIONS

I made these observations from 28 December through 12 January during winter 2000–2001 on the Superior National Forest (SNF) in northeastern Minnesota (47° 50′ N, 91° 25′ W) while attempting to capture gray wolves (*Canis lupus*) for radio collaring. I located radio-marked wolves from fixed-wing aircraft and then homed in on the location with hand-held telemetry immediately after landing. I used a manual prey distress predator call to attract wolves sufficiently close to dart them with anesthesia for capture and radio collaring. I called wolves at kill sites, non-kill sites, and sites where kill information was unknown. I approached wolves from downwind to a distance they would be able to hear and respond to the predator call. I concealed myself so that wolves would not immediately identify me when they approached, usually by backing into spruce (*Picea* spp.) or balsam fir (*Abies balsamea*) trees, which also concealed me from above. The predator call was then blown to imitate a dying rabbit or young deer. Notes were kept of the change of signal strength and other occurrences including ravens flying over.

The actual distance between my location and wolves was unknown and varied from site to site. Typically 6–25 ravens have been reported at wolf kills (summarized in Vustich et al. 2004) with as many as 80 being present in some cases (Carbyn et al. 1993); between 0 and 16 ravens have been reported in association with wolves away from kills (Stahler et al. 2002). I observed between one and five ravens responding to the predator call on 13 of 17 trials (76%) by flying within 100 m or directly over my location. Those that flew directly over me approached in a manner that suggested directed flight. Those that came within 100 m flew directly toward me and then changed course when they appeared to detect me. Ravens

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responded during all trials near known kill sites (n = 8), once when it was known there was no kill present (n = 3), and four of six times when kill information was unknown.

DISCUSSION

I observed ravens investigating a sound that simulates the distress cry of a dying animal. Ravens are known to use audible cues as a foraging technique (Heinrich et al. 1993, White 2005), but this behavior has not previously been reported regarding animal distress calls. Ravens congregate at wolf kill sites (Carbyn et al.1993, Stahler et al. 2002) and it can be assumed the eight trials at known kills were conducted in the proximity of ravens. The response rate of 100% (n = 8) to trials in the proximity of ravens suggests this may be an established foraging technique. Alternatively, ravens may have been investigating the simulated distress call out of curiosity. My observations are reported to present the possibility that ravens key on prey distress calls as one tool in a suite of foraging strategies. However, a more standardized study with controls is required to test for an effect. White (2005), in an experimental study, fired a rifle, blew an air horn, a whistle, and did nothing in an attempt to learn if ravens responded to gunshots. He found that ravens were attracted to the gunshot, but not the air horn or whistle. My observations were made incidental to another project and I did not have a control. White's (2005) results suggest the raven behavior I observed was in response to the distress call and not a response to a novel loud noise. White (2005) suggested that ravens might respond to gunshots because they associate the sound with other sounds that indicate potential food. It is possible prey distress calls are one such sound.

A carcass for ravens is an unpredictable food source on the landscape (Heinrich 1988, Stahler et al. 2002, Vustich et al. 2004). Using prey distress calls to find a carcass would likely increase a raven's resource intake and better insure an individual's survival.

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Hanging Behavior of the Hooded Crow (*Corvus cornix*)

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ABSTRACT.—We report observations of Hooded Crows (*Corvus cornix*) hanging upside down in the wild, for both playing and harvesting acorns. This behavior was recorded in six different events at the same site (Villa Chigi's urban park in Rome, Italy) and, in two cases, involved two individuals at the same time. Hanging behavior has been observed mainly in captive Northern Ravens (*Corvus corax*) and in few cases in wild corvids. Our observations indicate hanging behavior can be used to obtain food. These observations confirm that corvids have enormous plasticity that can be adapted to obtain food. *Received 5 March 2009. Accepted 19 July 2009.*

Play by birds is difficult to define and is a behavior that apparently has no purpose (Bekoff 1984, Heinrich 1999). Ficken (1977) noted that play is much more difficult to define in birds than in mammals. Birds may play socially, but only a few species exhibit the full range of play behaviors, from play chases to reciprocal object play (Fagen 1981, Ortega and Bekoff 1987). Some birds, such as corvids and parrots, exhibit more extensive social play than others (Fagen 1981, Iwaniuk and Pellis 2001). Corvids, among the Passeriformes, show the most complex play behavior including play with objects (e.g., objects carried into the air, dropped, and then caught with the beak many times), flight play, bathing play, vocal play, hanging (upside down posture from a branch holding with 1 foot, 2 feet or the beak), allospecific interactions, sliding, and 'snowromping' (e.g., a raven lay on its breast and slid head forwards downhill in the snow) (Ficken 1977, Moffett 1984, Heinrich 1990, Ratcliffe 1997, Heinrich and Smolker 1998, Brazil 2002).

Corvids may use cognitive tools in a way similar to apes, as reported in a study comparing mentality in these different animal groups (Emery and Clayton 2004). In fact, corvids have a brain significantly larger than in other birds and, in proportion, their brain has similar size as that of the chimpanzee (*Pan* spp.). Emery and Clayton (2004) concluded that cognition in corvids and apes must have evolved through a process of divergent brain evolution with convergent mental evolution. Heinrich and Bugnyar (2005) studied the acquisition of problem-solving behavior in captive ravens. Their results support the idea that behavior of ravens in accessing meat on a string is not only a result of rapid learning, but may involve the understanding of cause-effect relation between string and food.

Corvids and parrots can perform upside down hanging behavior, which can be considered as play (Elliot 1977, Ortega and Bekoff 1987, Heinrich and Smolker 1998, Diamond and Bond 2003). Hanging behavior has been observed in captivity many times in Northern Ravens (*Corvus corax*) (e.g., Gwinner 1966, Coombs 1978, Heinrich and Smolker 1998), but only a few records have been reported for corvids in the wild (McIntyre 1953, Gwinner 1966, Elliot 1977, Heinrich and Smolker 1998, Melletti 1999). Hanging behavior is primarily a type of play performed by highly social birds, such as corvids and parrots, which have the largest brain volume (Heinrich and Smolker 1998, Diamond and Bond 2003, Emery and Clayton 2004). Hanging behavior can be adopted for purposes other than play, but most reasons for this behavior remain unknown (Coombs 1978). Gwinner (1966) reported ravens performing hanging behavior to store food in an aviary and Melletti (1999) recorded a case of hanging behavior, lasting up to 5 min, in a wild raven for five consecutively times without apparent reason.

Corvids have the ability to access food that is difficult to reach, in particular ravens in captivity (Heinrich 1995, Heinrich and Bugnyar 2005). Our observations show that Hooded Crows (*Corvus cornix*) are able to obtain acorns otherwise difficult to access from an upright posture. Use of hanging behavior by Hooded Crows demonstrates the ability to solve a problem. To our knowledge this is the first observation reported of

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FIG. 1. Hanging behavior of Hooded Crows while feeding. Photograph by Mario Melletti.

hanging behavior in wild Hooded Crows with the intent to obtain food. Little is still known about this behavior.

OBSERVATIONS

We made observations of hanging behavior by Hooded Crows from October 2005 through October 2006 in the urban park of Villa Chigi in Rome, Italy. The park is 5 ha in size and it is characterized by Stone pine (*Pinus pinea*), Holm-oak (*Quercus ilex*), and open meadows. Data were collected weekly for 6 hrs/week divided between morning and afternoon (total number of hrs = 288). We conducted the study using 10× binoculars and a digital camera.

Hooded Crows were observed for 96 of 288 hrs during which hanging in upside down posture was observed in six different events: two on 7 November 2005 (2 individuals), one on 14 January 2006 (1 individual), one on 6 October 2006 (1 individual), and two on 26 October 2006 (2 different individuals). Hanging behavior lasted from a few seconds up to 1 min during which birds held the wings pressed to the body and the head was held both horizontally and vertically (Fig. 1).

DISCUSSION

Hanging behavior was observed by McIntyre (1953) for wild Carrion Crows (*Corvus corone*), Gwinner (1966) and Heinrich and Smolker (1998) for captive Northern Ravens, and Elliot (1977) and Melletti (1999) for wild Northern Ravens. Hooded Crows would hang upside down with one foot and then land upright on the ground. We observed two Hooded Crows that performed this behavior alternating one and both feet while hanging upside down. A Hooded Crow in hanging posture was imitated by another bird on two occasions, which performed the same posture at the same time. Gwinner (1966) reported similar cases of imitation in captive ravens.

We observed hanging behavior by Hooded Crows in three events that seemed as play, as described by other authors (Gwinner 1966, Heinrich and Smolker 1998), while in three other occasions the goal of the crows was to reach acorns of Holm-oaks, which were eaten or stored in the ground. Acorns were located on small twigs and upside down posture might seem to be the only way for crows to obtain them. The upright posture probably was not the best way to pick

acorns, because the twigs were not sufficiently strong to support the weight of crows in that position. By hanging upside down, crows were able to obtain acorns with their beak, before coming back to the ground. They remained upside down for few seconds. These observations indicate that hanging behavior is not only a type of play, but can be used to reach food, as also reported by Gwinner (1966) for captive ravens. Elliot (1977) suggested the hanging behavior of ravens was for display by courting males. These observations confirm that corvids have huge plasticity that can be adapted to solve different situations.

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Conspecific Brood Parasitism by the Dickcissel

Brian D. Peer[1]

ABSTRACT.—I report the first observation of conspecific brood parasitism in the Dickcissel (*Spiza americana*). I monitored 302 nests during a study of the interactions between parasitic Brown-headed Cowbirds (*Molothrus ater*) and Dickcissels. This and a possible second case of conspecific brood parasitism may have resulted from females laying in nests after their original nests were destroyed in nearby hayfields. *Received 9 June 2009. Accepted 4 September 2009.*

Avian brood parasites lay their eggs in nests of other individuals thereby avoiding costs associated with parental care. Obligate brood parasites such as the Brown-headed Cowbird (*Molothrus ater*) lay their eggs in nests of other species (Peer et al. 2005), whereas conspecific brood parasites lay in nests of individuals of the same species (Yom-Tov 1980). Conspecific brood parasitism (CBP) has been reported in 236 species (Yom-Tov 1980, 2001) and tends to be most common in precocial species such as waterfowl, colonial species, and species with specialized nest sites such as cavities (Yom-Tov 1980, 2001; Rohwer and Freeman 1989).

Females may practice CBP to increase their fecundity by laying extra eggs in nests of other individuals, in addition to tending their own clutches (Sorenson 1991, Lyon 1993). Alternatively, females that do not have a nest may attempt to make the best of a bad situation and lay their eggs in nests of other females or, if their nests are destroyed during the laying cycle, they may lay eggs in nests of nearby neighbors (Hamilton and Orians 1965, Feare 1991; but see Rothstein 1993, Peer and Sealy 2000). I report the first known instance of CBP in the Dickcissel (*Spiza americana*).

METHODS

I monitored Dickcissel nests at a reclaimed mine from 2006 to 2008 in southern McDonough County, Illinois, USA during a study of the interactions between Brown-headed Cowbirds and their Dickcissel hosts. Dickcissel nests were inspected for presence of cowbird eggs and to record the Dickcissel's response to parasitism. Most nests were checked daily, and each egg was numbered. Nests were checked beginning at least 3 hrs following sunrise, after the time of day Dickcissels typically lay (unpubl. data). I checked nests sufficiently late to avoid missing an egg being laid 1 day and returning the second day and finding two additional eggs; this could lead to the erroneous conclusion that a second female laid in the nest. Dickcissels nested in grasslands planted as part of the mine reclamation and were surrounded by agricultural fields that included hay in which the Dickcissels also nested. Nests in hayfields were not monitored because the hay was mowed once a month destroying the nests.

RESULTS

A total of 302 Dickcissel nests was monitored. Modal clutch size was four eggs with a range of three to seven eggs. Nest #41 was found in the afternoon of 24 June 2008 with four eggs and I numbered all eggs at this time. Seven eggs were in this nest on 26 June. Because birds lay no more than one egg per day (Johnson 1999), at least one additional female laid an egg in this nest. The hayfields immediately adjacent to this nest were mowed the afternoon of 24 June. The nest contents remained the same until 3 July when five eggs had been removed, and two eggs remained. The nest was subsequently deserted.

DISCUSSION

This is the first reported observation of Conspecific Brood Parasitism (CBP) in Dickcissels. The rarity of CBP in this species is not surprising because Dickcissels do not demonstrate traits associated with conspecific brood parasites. What caused the parasitism that I observed? Dickcissels at my site nested in grasslands and in adjacent hayfields. The hayfields were mowed regularly during the breeding season and in 2008 the hay adjacent to nest #41 was mowed in the days prior to the parasitic event. It is possible the

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parasitic female was nesting in the hayfield and her nest was destroyed by the mowing, after which she laid one of her remaining eggs in nest #41. However, I did not monitor nests in hayfields and I did not ascertain the genetic identities of the eggs. Thus it is unclear whether nest destruction precipitated this case of CBP. Birds may make the best of a bad situation by laying an egg in another nest if their own nests are destroyed during the laying stage (Hamilton and Orians 1965). Conspecific brood parasites such as European Starlings (*Sturnis vulgaris*) and Wood Ducks (*Aix sponsa*) lay in nests of conspecifics after their nests have been destroyed or experimentally removed during the laying cycle (Haramis et al. 1983, Feare 1991). Species not known to practice CBP (Red-winged Blackbird [*Agelaius phoeniceus*], Great-tailed Grackle [*Quiscalus mexicanus*]) do not lay parasitically after their nests have been experimentally removed (Rothstein 1993, Peer and Sealy 2000). Illinois was mostly grassland prior to European colonization. Today <1% of the original grassland habitat remains (Iverson 1988) and there is little suitable nesting habitat for Dickcissels and other grasslands birds (e.g., Herkert 2003). The density of Dickcissels at my site was high (upubl. data), possibly due to lack of suitable habitat in the western Illinois region. Dickcissels may nest in suboptimal habitat such as hayfields that are mowed causing nest failure during laying. These females may have responded by laying in nests of nearby females, which is a better strategy than dumping physiologically committed eggs indiscriminately in the environment.

The seven-egg clutch at this nest is the largest reported clutch for the Dickcissel, one egg more than what had been reported previously (Temple 2002). I also observed a second nest with a seven-egg clutch. On 26 June 2006 nest #81 was found with four eggs. On 28 June it contained six eggs, on 29 June seven eggs, and the contents remained the same until the eggs hatched. There were no laying irregularities during the time I monitored the nest that would suggest CBP, but a second female could have laid an egg in the nest before I found it on 26 June. This is only the second time a seven-egg clutch has been reported for this species and the other was a result of CBP.

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First Report of Olrog's Gull Depredation by Sympatric Kelp Gulls

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ABSTRACT.—We observed adult Kelp Gulls (*Larus dominicanus*) capture and eat Olrog's Gull (*L. atlanticus*) chicks in the Bahía Blanca estuary, Argentina. This estuary holds the largest breeding colony of Olrog's Gulls. There are no previously published reports of Kelp Gulls capturing and eating Olrog's Gull chicks. Our data support suggestions made by other authors about the possible existence of conflicts in colonies where both species breed in close proximity. *Received 13 March 2009. Accepted 7 October 2009.*

Olrog's Gull (*Larus atlanticus*) (Olrog 1958) is endemic to the coastal wetlands of the Atlantic Coast in Argentina, Uruguay, and southern Brazil (Yorio et al. 2005), and is listed as a Vulnerable species (Birdlife International 2008). Factors that led to this classification include the limited geographical range of the species, small estimated population size (4,000–5,000 pairs), its specialized diet, and high susceptibility to anthropogenic changes in the environment.

Few Olrog's Gull breeding sites have been identified, and all are in Argentina (Yorio et al. 2005). Over 80% of the total breeding population is concentrated in the Bahía Blanca estuary with the largest colony (~3,600 pairs) on Isla del Puerto (38° 48′ S, 62° 15′ W) surrounded by a colony of Kelp Gulls (*L. dominicanus*) (Delhey et al. 2001). The estimated size of the later was ~5,000 pairs in 2003 but appears to have grown considerably since then (P. F. Petracci, pers. comm.).

There is only one previous report of depredation attempts by Kelp Gulls on Olrog's Gull eggs and chicks (Petracci et al. 2004), and no reports of successful depredation were found during a literature search. This is the first report of Olrog's Gull chicks as prey of adult Kelp Gulls.

OBSERVATIONS

We monitored depredation of Olrog's Gull eggs and chicks in the Isla del Puerto breeding colony in 2005, 2006, and 2007. We studied the colony in 2005 during part of the egg-laying phase (29 Sep–7 Oct) and part of the hatching and chick-rearing periods (27 Oct–15 Nov) and, in 2006 and 2007, during the early hatching and chick-rearing periods (17 Oct–9 Nov and 1 Oct–1 Nov, respectively). We spent ~8 hrs per day in the colony between 0800 and 1200 hrs ST, and between 1500 and 1900 hrs. We did not observe direct egg depredation in any year but did observe depredation of Olrog's Gull chicks in 2006 and 2007. We observed two depredation events in 2006, one on 20 October (1015 hrs) and the other on 1 November (1945 hrs). We observed six depredation events in 2007: 21 October (1800 hrs), 22 October (1905 hrs), 27 October (1715 hrs), 28 October (1045 hrs and 1910 hrs), and 30 October (2018 hrs).

Adult Kelp Gulls usually made fast, low-flying passes over the Olrog's Gull colony and used their beaks to snatch chicks from or around their nests. We observed one Kelp Gull drop the Olrog's Gull chick while hovering above the colony, causing the death of the chick shortly after its impact with the ground. We calculated all depredated chicks were ~10 days of age based on body size. We strongly suspect the same Kelp Gull was responsible for four of the six events observed in 2007. This Kelp Gull returned to the same nest ~4 m from the Olrog's Gull colony while eating the chicks. Adult Olrog's Gulls did not display defensive behavior during the attacks, nor while Kelp Gulls fed on chicks a short distance from the Olrog's Gull colony.

DISCUSSION

Kelp Gull populations are expanding throughout most of their geographical range (Yorio et al. 2005), and their generalistic/opportunistic feeding habits are thought to have an important role in this expansion (Giccardi et al. 1997). The negative effects of expanding Kelp Gull populations on

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other seabird species has been associated with increased artificial food sources (McGehee and Eitniear 2007). One study conducted at six colonies, where both Kelp and Olrog's gulls breed, indicated these species share many microhabitat characteristics, and suggested the presence of spatial conflicts between them (García Borboroglu and Yorio 2007a, b).

Isla del Puerto is within an international deepwater port and 3.2 km from the city of Bahía Blanca (~450,000 inhabitants). Discarded fish from a small-scale fishing fleet and presence of open-sky refuse tips, slaughter houses, and pork and poultry production systems near these colonies provide readily available and abundant food sources throughout the year, and might sustain growth of this colony (Petracci et al. 2004). This could lead to increased predatory pressure by Kelp Gulls on Olrog's Gulls.

Individual specialization as predators of seabird chicks and eggs has been reported for a number of marine birds including Kelp Gulls (Yorio and Quintana 1997, Quintana and Yorio 1998), other gull species (Harris 1965, Hatch 1970, Parsons 1971, Fuchs 1977, Hulsman 1977), and Great Skuas (*Stercorarius skua*) (Votier et al. 2004, 2007). In our study, it is likely the series of consecutive predatory attacks observed in 2007 was by a single specialist Kelp Gull.

Our observation of eight chicks depredated over a 3-year period would not suggest substantial pressure on this Olrog's Gull colony. However, we provide sufficient evidence to suggest further studies that accurately quantify the impact of depredation and other possible conflicts between these species.

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Second and Third Records of Snares Penguins (*Eudyptes robustus*) in the Falkland Islands

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ABSTRACT.—The Snares Penguin (*Eudyptes robustus*) breeds only on the Snares Islands, New Zealand, and is vagrant throughout the New Zealand region and southeast Australia. The only previous record outside this area was one in the Falkland Islands in 1988. We report the unusual occurrence of two Snares Penguins in the same colony in the Falkland Islands in 2008, and discuss identification issues. Vagrant penguins demonstrate the incredible dispersal ability of these flightless birds. *Received 9 March 2009. Accepted 19 July 2009.*

Snares Penguins (*Eudyptes robustus*) are endemic to New Zealand, breeding only on the Snares Islands (48° 00′ S, 166° 33′ E), and straying to surrounding islands, south-east Australia, and Tasmania (Marchant and Higgins 1990, Williams 1995). They are absent from their breeding areas during winter, when they are probably pelagic and migratory. Snares Penguins are rarely observed away from the Snares Islands and their movements are poorly known (Marchant and Higgins 1990). The occurrence of at least five Snares Penguins in the Chatham Islands in January and February 2003 was considered exceptional (Miskelly and Bell 2004, Miskelly et al. 2006). The only previous record of this species beyond Australasia was an adult in the Settlement Rookery on New Island (51° 43′ S, 61° 17′ W) in the Falkland Islands on 10 December 1988 (Lamey 1990, Martínez 1992). We discuss the unusual occurrence of two Snares Penguins in the same colony in the Falkland Islands 20 years later.

OBSERVATIONS

We visited daily the Settlement Rookery on New Island during the entire breeding season during the course of scientific studies of Western Rockhopper Penguins (*Eudyptes chrysocome*) (Poisbleau et al. 2008). An adult Snares Penguin was found on 30 November and 1 December 2008 (Fig. 1). The rookery was visited every day until the middle of January 2009, but the bird was not seen again. However, a second bird was observed on 24 and 25 December 2008 (Fig. 2). We captured both birds to take standard measurements (Table 1). The appearance of the birds was sufficiently different to be certain they were not the same individual; the second bird was larger, the black color of its head was duller, it had a partially gray chin, its crests were very short, the pink color of its gape and of the skin around its beak was less obvious, and its eyes were brownish (not red) even under strong light.

DISCUSSION

The identification of extra-limital Snares Penguins requires care. The following characteristics allow separation from Western Rockhopper Penguins (Shirihai 2007): a wider yellow stripe above the eye starting close to the beak, an obvious pink gape and skin along the edge of the lower mandible, a larger and more bulbous beak, the absence of a black crest on the rear crown, a shorter yellow crest less pendulous behind the eye, a bold black tip on the underside of the flipper, and an overall larger size. The large beak and overall size, and the pink gape and skin along the beak could also resemble a hybrid between a Rockhopper Penguin and a Macaroni Penguin (*Eudyptes chrysolophus*). Several instances of such hybridization have been documented in the Falkland Islands (White and Clausen 2002). However, the shape of the yellow stripe and crest of the birds that we found were typical of Snares Penguin and completely different to those of Rockhopper or Macaroni penguins or postulated hybrids between them.

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FIG. 1. Adult Snares Penguin (right) next to a Western Rockhopper Penguin on New Island, Falkland Islands, 30 November 2008. Photograph by Laurent Demongin.

A Snares Penguin could also be mistaken for an Erect-crested Penguin (*Eudyptes sclateri*), a species that breeds on the Antipodes and Bounty islands southeast of New Zealand (Marchant and Higgins 1990) and that occasionally reaches the Falkland Islands (Strange 1982, Summers 2005), including one that bred with Rockhopper Penguins on Pebble Island (120 km northeast of New Island) between January 1997 and January 2008 (Morrison et al. 2005, Arnold 2008). Erect-crested Penguins have crests that are erectile and nearly parallel when seen from the front (Marchant and Higgins 1990) while Snares Penguins have crests that droop behind the eye, and forms a V when seen from the front. Erect-crested Penguins also have a different head shape with a domed crown, and larger chin reaching closer to the beak tip (Shirihai 2007). Cases of hybridization between Erect-crested and Rockhopper penguins have been reported at the Falkland Islands (Napier 1968) but the descendants were not described. An apparent Erect-crested x Rockhopper hybrid seen next to the Erect-crested Penguin on Pebble Island in January 2006 looked similar to the birds that we saw, but differed in having the extended chin profile of an Erect-crested Penguin, and black feathers in the crest (a Rockhopper characteristic). Other details of the superciliary stripe and bare skin at the gape also matched Western Rockhopper or Erect-crested penguins rather than Snares Penguins (C. M. Miskelly, pers. comm.).

The first bird we found, based on measurements and plumage patterns, was probably an adult female whereas the second was probably an immature male. The beak of the second bird was much longer and was not as deep. The beak shapes were quite different, the first one being bulbous with parallel edges while the second was less robust and more slender. The latter beak shape is typical of immatures; the more massive beak of adults is achieved during the third or later years (Stonehouse 1971).

The weight of crested penguins varies seasonally with the heaviest birds being recorded before the molt (Warham 1975). The weight of the

FIG. 2. Immature Snares Penguin (right) among Western Rockhopper Penguins on New Island, Falkland Islands, 24 December 2008. Photograph by Laurent Demongin.

second bird we found exceeded the range of breeding Snares Penguins (Stonehouse 1971) but fit well with pre-molting immature males (Warham 1974a).

Most vagrant crested penguins are sub-adults recorded before or during their molt (Woehler 1992, Miskelly and Bell 2004), like the bird we observed on 24–25 December. The two other Falkland Islands records of Snares Penguin (including our first bird) were adults during the breeding season. However, observers rarely visit the rookeries after the end of the breeding season,

TABLE 1. Measurements (following Warham 1975) of the two Snares Penguins found in the Falkland Islands in 2008, and comparison with $\bar{x}$, (*n*), and [range] data from (a) Stonehouse (1971) and (b) Warham (1974b).

			Adult male		Adult female	
Characteristic	Bird 1	Bird 2	(a)	(b)	(a)	(b)
Flipper, mm	181	191	183 (61) [170–193]	184.0 (114)	177.3 (47) [167–187]	178.8 (82)
Beak length, mm	54.2	57.1	59.2 (68) [54–69]	59.1 (35)	52.5 (58) [49–61]	52.0 (12)
Beak depth, mm	23.3	22.6		28.2 (35)		24.2 (12)
Head and beak length, mm	122.6	127.9				
Mass, g	3,300	4,360	3,320 (41) [2,450–4,300]		2,780 (32) [2,300–3,400]	

and vagrant birds coming ashore to molt could easily be missed.

The Chatham Islands are only ~1,400 km from the Snares Islands, and yet the presence of several Snares Penguins in 2003 was considered anomalous, possibly reflecting a changed at-sea distribution (Miskelly and Bell 2004). It is difficult to assess the reasons for the presence of this species in the Falkland Islands, ~8,000 km from the Snares Islands. However, the occurrence of penguins endemic to the New Zealand region in the Falkland Islands demonstrates their incredible dispersal ability. The opposite is also true with Western Rockhopper Penguins reported from the Snares Islands south of New Zealand (Tennyson and Miskelly 1989, Miskelly et al. 2001).

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A New Bird Species for Costa Rica: Sapphire-throated Hummingbird (*Lepidopyga coeruleogularis*)

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ABSTRACT.—I present the first confirmed record of the Sapphire-throated Hummingbird (*Lepidopyga coeruleogularis*) at Punta Banco, southwestern Costa Rica. An adult male was seen and photographed perched on a twig at the border of a second growth forest tract. This observation extends the geographic distribution of this species from northern Colombia to southwestern Costa Rica. *Received 28 February 2009. Accepted 27 August 2009.*

The Sapphire-throated Hummingbird (*Lepidopyga coeruleogularis*) is known to occur from western Panama to northern Colombia, along most of the Pacific slope and over the eastern region of the Caribbean slope of Panama into Colombia. This hummingbird is more abundant in coastal forests (Ridgely and Gwynne 1989), occupying primarily secondary forests and scrubby clearings, and in lower frequency, around mangrove patches. It is usually observed foraging for both nectar and insects at low strata (Ridgely and Gwynne 1989, Stiles et al. 1989).

This species is known in Costa Rica from an old and possibly mislabelled specimen and from an unconfirmed record from 1962 (Stiles et al. 1989). Since then, this species has not been reported for Costa Rica (Obando-Calderón et al. 2007).

OBSERVATIONS

An adult male Sapphire-Throated Hummingbird was observed foraging and photographed on 2 April 2008 at Tiskita Jungle Lodge landing strip at Punta Banco, Costa Rica (8° 21′ N, 83° 06′ W) (Fig. 1). This area is ~10 km from the Panamanian border. Possibly the same male was observed the previous day, foraging at the same spot. The hummingbird was feeding on flowers of a vine of the Rubiaceae family growing near the lodge's airstrip. The area is an open field surrounded by patches of secondary forest and early second growth vegetation, numerous ornamental plants in the lodge's gardens, and an extensive living fence of flowering *Ibiscus rosa-sinensis*, which attracts several other species of hummingbirds.

On 23 December 2008 a new report of this species was made by Kevin Easley even further into Costa Rica, ~35 km from the Panamanian border at la Gamba near Golfito. This region is comprised of extensive pastures with living fences and isolated trees surrounded by mature protected forest on the slopes that surround the valley. The species was seen visiting flowers of garden plants and living fences.

DISCUSSION

This is one of several bird species, typical of open areas that have been recently reported in Costa Rica, possibly coming from Panama (Stiles et al. 1989; Sánchez et al. 1998; EB, unpubl. data). The range expansion of these species may be caused by the increasing destruction of the natural mature forests in the region during the last decades (Sanchéz-Azofeifa et al. 2001, 2003). Most of the original forest has been eliminated in the lowlands of Central América and replaced by pastures or agricultural fields, allowing some birds to expand their original range. The Sapphire-throated Hummingbird is expected to soon become more common along the Costa Rican Pacific Coast, given its use of open areas and behavior.

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FIG. 1. Male Sapphire-throated Hummingbird in Costa Rica's Pacific Coast (photograph by Saul Bocian).

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Ornithological Literature

Robert B. Payne, Review Editor

THE CURSE OF THE LABRADOR DUCK. MY OBSESSIVE QUEST TO THE EDGE OF EXTINCTION. By Glen Chilton. Simon & Schuster, New York, USA. 2009: x + 305 pages, 10 black and white figures, 1 map. ISBN: 978-1-4391-0247-3; 978-1-4391-2499-4 (ebook). $25.00 (hardcover).—For those whose interest in birds extends beyond another tick on their life list, extinct birds often provide a source of intense fascination. Each species has its own allure, but one that is also coupled with an air of unattainability, like a photograph of a beautiful woman on the obituary page. The Labrador Duck (*Camptorhynchus labradorius*), the first endemic North American bird to disappear historically, about 1875, remains one of the most perversely enigmatic of extinct birds. Although known from a fair number of specimens (at least 55 still exist), few have reliable data and virtually nothing is known about the breeding of the species or its summer distribution. It has escaped the attention of monographers such as have labored over the Great Auk (*Pinguinus impennis*), Passenger Pigeon (*Ectopistes migratorius*), and Carolina Parakeet (*Conuropsis carolinensis*).

Enter Glen Chilton, who debuted in ornithology on the bandwagon of studies of song dialects of the White-crowned Sparrow, which led to his being an author on the account of *Zonotrichia leucophrys* in the *Birds of North America* series. Lured by the prospect of a gratis set of that costly work, he chose to write another species account and what could possibly have been easier than the Labrador Duck, about which so little was known? With the account of the Labrador Duck under his belt, Chilton became its de facto "authority," thus setting the stage for his "obsessive" quest to examine every specimen of the species, perhaps not unlike the person who patronized every Starbucks coffee shop in the world to set a record.

This book is about Chilton's visits to museums scattered through Europe and North America to view specimens of Labrador Ducks. The opposite of a work of scholarship, it is very much a travelogue, and a tedious one at that. From the author's web site we learn that Chilton wants people to believe that he is a bon vivant engaged in "outrageous adventures," which in this case means going to a distant city, measuring a "stuffed duck," and then wandering about town in search of alcohol and vegetarian food (to me, the thought of eating tofu in Paris and Vienna is more depressing than the fate of the Labrador Duck). The title, of course, is a gimmick, the only curse being the book itself. Nor does the subtitle make much sense considering that the Labrador Duck is long past the edge of extinction.

Chilton's background and attitude did little to prepare him for museum work, as he plainly knows next to nothing about collecting or preparing birds. The specimens he looked at met their ends by being "blasted," "blown to kingdom come," or shot full of "bullets," which, if true, would have left little for him to examine. Although he includes brief instructions on preparation techniques taken from a museum pamphlet, he seems not to understand the process and refers more than once to the incision through which the "guts were pulled out." Specimens are invariably "stuffed," a word generally avoided by museum ornithologists but apparently deliberately overused by Chilton to convey his poorly disguised disdain for museums as places full of "stuffed" dead things. Not being knowledgeable of the history of museum ornithology, Chilton is bound to have overlooked facts that would be evident to someone with more experience. What else could one expect from one for whom the name Verreaux carried no significance? We also read (page 304) that: "In November of 1844, Colonel Nicolas Pike shot a drake Labrador Duck at the mouth of the Ipswich River at the south end of Plum Island, New York. History doesn't say whether or not the duck was doing anything to provoke the colonel. Perhaps Pike just really, really hated ducks". Not only is this gratuitously stupid, but Chilton shows no evidence of recognizing the identity of Nicolas Pike nor of Pike's connection with other extinct birds (*Subtropical Rambles in the Land of the Aphanapteryx*, 1873).

Chilton provides a brief description, usually only a paragraph, mostly detailing defects, of the various specimens of Labrador Duck. In a few instances he appears to have unearthed some new

information on the history of a given specimen, which is commendable. But most of the book is simply an ego-indulging procession of irrelevancies. Why do we need to know that he was a breech birth, a nervous and obsessive child, and that on at least four occasions in his duck travels he shared a room, or even a bed with various young women who were not his wife? Chilton seems to regard himself as quite a humorist, but his humor is so tiresomely puerile as to make George Gobel and Dave Barry seem like genuine wits. Pick any pejorative adjective that describes annoying prose and it will apply somewhere in this book: arrogant, facetious, facile, flippant, glib, precious, sophomoric, and snotty. Throughout, Chilton manages to be condescending or even downright insulting to individuals, institutions, and entire countries. I daresay that following the appearance of this book he will be unwelcome in many places where he was once treated with courtesy and respect.

Errors large and small throughout the book call into question the accuracy of almost anything Chilton writes. For example, the Portuguese word for "cultivator" is *lavrador*, not *llavrador* (incidentally, Chilton seems to revel in his ignorance of languages). Some older bird specimens were preserved with arsenic, not cyanide. There are no sea lions, large or small, around Grand Manan Island or anywhere else in the North Atlantic. The national mall in Washington does not run just from the Capitol to the Washington Monument, which latter he has apparently confused with the Lincoln Memorial. It seems intended that the book not be consulted again after its first reading, as there is no table of contents, no index, and no bibliography.

As partial recompense for inflicting this fulsome blot on the literature of extinct birds, Chilton owes ornithology and the staffs of all the museums he visited an exceptionally scholarly and insightful monograph on the Labrador Duck. Considering that he was ill equipped to undertake such an endeavor in the first place, I doubt that he will ever be able to make satisfactory repayment of his debt.—STORRS L. OLSON, Curator, Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA; e-mail: olsons@si.edu

BIRD BANDING IN NORTH AMERICA: THE FIRST HUNDRED YEARS. Edited by Jerome A. Jackson, William E. Davis Jr., and John Tautin. Nuttall Ornithological Club, Cambridge, Massachusetts, USA, 2008: ix and 280 pages, 62 figures and photographs. ISBN: 1-877973-45-9. $40.00 (cloth).—This volume brings together contributions presented at a symposium which occurred at the North American Ornithological Conference in New Orleans in 2002. The symposium commemorated 100 years of scientific bird banding in North America, the birth of which is designated by the banding of Black-crowned Night-herons (*Nycticorax nycticorax*) by the Smithsonian Institution's Paul Bartsch in 1902. The 12 chapters trace the trajectory of bird marking from modest but enthusiastic beginnings through the wide variety of scientific pursuits that have used this important ornithological tool.

The first three chapters provide historical perspective. Chapter 1 gives the early history of bird banding in North America. It starts with a bit of background on marking birds in the 16th century in the Old World, and quickly settles in North America, relating the well-known story of John James Audubon's 1804 experiment of marking Eastern Phoebes (*Sayornis phoebe*) with silver wire. This is followed by an interesting overview of the factors that led to the popularity of nature study in general and bird marking in particular in the early 20th century – including such disparate elements as increased leisure time due to the availability of electricity and the sudden accessibility of aluminum. The chapter goes on to the more specific underpinnings: the genesis of organized banding, founding of the American Bird Banding Association and the first banding stations, and finally the federal government's role in recognizing and controlling banding in the United States

Chapter 2 discusses the role of banding organizations in education and training of banders; the distribution of data, techniques, and materials; and in encouraging regional cooperation. The organizations mentioned include national (including the present North American Banding Council) and regional groups, as well as major bird observatories and banding station networks. They are arranged by type with a brief summary of each group's history and function.

Chapter 3 focuses on the history of the Bird Banding Laboratory (BBL). The BBL wasn't formally designated as such until 1961, but this chapter begins in 1920, when Frederick Lincoln was charged by the USDA Bureau of Biological Survey with organizing their "banding office."

He remained in this position until 1946 and is noted as the true founder of the modern bird banding program. The chapter proceeds to tell the history of the BBL by decade, ending in 2002, which coincided with the retirement of the BBL's sixth Chief and chapter author John Tautin.

The rest of the book provides overviews of the role of bird banding in various research areas, focusing on particular instances where banding has made important scientific contributions. These include population monitoring and ecology, rare species recovery, migratory game bird and waterbird conservation, avian ecotoxicology and disease, habitat use, and behavioral research. The chapters overall make a fine case for the value of bird banding, even though, as several authors point out, the original intent was focused primarily on bird movements. Most chapters conclude with recent developments and future directions in each area, and how banding might fit into these new horizons.

The chapters in this compendium vary in form from chronologies and narratives to something more resembling typical scientific style. Every chapter ended with literature cited, a convention I prefer over paging to the end of the entire volume to look up a reference. I wasn't able to discern whether there was any particular order to the chapters past the first three, which dealt with history. The volume might have flowed a little better if the chapters had progressed from broad research themes to more specific studies, or perhaps followed some chronological order. I found only one major editing gaff. In Chapter 5, a concluding paragraph was printed twice, once at the end of a series of species accounts, and again three paragraphs later at the end of the chapter.

There are 62 black-and-white figures in the book, mostly photographs. Many of them are "mug shots," generally of historical figures or researchers whose work is featured in the chapter. I often don't notice these things, but in this volume I could not help being struck that over half of the photos featured white guys, mostly middle-aged. There were a few women, and no people of color. Are bird banding and ornithology really that devoid of ethnic, racial, and gender diversity? Yikes. We have something to work toward in the next hundred years.—JULIE A. CRAVES, Rouge River Bird Observatory, University of Michigan-Dearborn, Dearborn, MI 48128, USA; e-mail: jcraves@umd.umich.edu

INGESTION OF LEAD FROM SPENT AMMUNITION: IMPLICATIONS FOR WILDLIFE AND HUMANS. By Richard T. Watson, Mark Fuller, Mark Pokras, and W. Grainger Hunt. The Peregrine Fund, Boise, Idaho, USA. 2009: 383 pages. ISBN: 0-9619839-5-7. $ None shown. (paper).—As a rule, conference proceedings are uninspiring tomes. The ugly stepchildren of the academic publication family; their contents are often limited to progress reports of ongoing research, literature reviews, and the results of short-term Master's Degree research projects. There are some conferences, however, for which a published proceedings is not only appropriate, but also provides an exceptionally useful resource for a wide audience. The proceedings of the conference *Ingestion of Lead from Spent Ammunition: Implications for Wildlife and Humans*, held 12–15 May 2008 at Boise State University is one of these. The book fully addresses the ubiquitous nature of lead toxicity by including voices from science, medicine, policy, and business. Whereas it would be difficult to find one scientific journal that would accept this breadth of viewpoints, the proceedings format allows for the cross-disciplinary compilation of knowledge necessary to put the lead issue in context.

Everyone knows something about the toxic effects of lead but few know everything about it. For example, most Americans know that in the 1970s, awareness of the effects of lead on human health resulted in its removal from house paint and gasoline. Hunters know that in 1991, documented adverse effects of lead ingestion on eagles and waterfowl species resulted in regulations outlawing lead shot for waterfowl hunting. *Ingestion of Lead from Spent Ammunition* provides information of which most people are not aware, such as: how lead is toxic (in a fascinating paper by Pokras and Kneeland); effects of low-dose exposure of lead on humans who consume hunted game; and the magnitude of the problem in terms of the amount of lead released into the environment by outdoor sports (6–10 thousand metric tons annually in the U.S.) or the number of species known to have incidences of high lead levels (over 130 species of vertebrates).

The unique strength of this book is it's "conservation medicine" approach which Pokras and Kneeland (page 7) define as "examin[ing] the linkages among the health of people, animals, and the environment". Imagine the value to wildlife rehabilitation veterinarians when they tap into the

rich field of lead exposure in human development, and vice versa; or the public health official who becomes familiar with the work on retention of lead fragments in hunted wildlife. Proof of this book's integrated approach to lead is the diversity of author affiliations: wildlife research centers, zoos, environmental agencies and non-profits, human medicine, and state conservation offices, to name a few.

The book is composed of 53 papers (25 peer-reviewed, 10 not peer-reviewed, and 18 extended abstracts) organized in four main sections: review of lead uptake and toxicosis in humans and wildlife; lead exposure in humans from spent ammunition; lead exposure, sources, and toxicosis in wildlife; and, remediation of lead exposure from spent ammunition. There are also nine expert commentaries transcribed from the meeting and an introduction and conference summary by the esteemed raptor biologist Ian Newton. Birds, especially raptors, are the predominant taxonomic group in the research. Not surprisingly, work on the California Condor (*Gymnogyps californianus*) is well represented. Other bird species addressed include Golden Eagles (*Aquila chrysaetos*) and fish eagles (*Haliaeetus* spp.), waterfowl, doves, and other terrestrial birds.

Geographically, most papers concern the United States, but there is good representation from Europe. In the one paper from South America, Saggese et al. review lead toxicosis in raptors from Argentina. In discussing sources of lead in the environment, they cite the recent and growing popularity of dove and pigeon hunting in central Argentina where, absent any limits on the number of birds killed, hunters regularly discharge over 1,000 cartridges per day, killing or injuring as many birds. The barbarism of these hunts is, therefore, compounded by the 1,600 metric tons of lead released into the local environment each year and the fact that crippled and dead birds are left for scavengers (including humans) to consume, lead shot and all.

There are only two minor flaws with the book. The first is the repetition of basic information in many of the papers. One would only notice this if the book was read cover-to-cover, a method for which the book was not designed. The second flaw concerns the 18 entries that are extended abstracts. Some of these are quite extensive with figures and tables, etc. while others aren't 'extended' at all. Either way, no one likes to cite abstracts and when I searched for full papers that these abstracts should have evolved into by now I wasn't able to find any.

In his closing comments for the meeting, Ian Newton noted the conference showed that lead from spent ammunition poses a bigger human health problem than previously recognized. Indeed, after reading this book, one cannot help but be alarmed at the widespread and insidious nature of lead ingestion by humans and wildlife. These proceedings are a call for action and, unlike many environmental problems that seem insurmountable; the removal of lead from outdoor sporting equipment is attainable.

The book is published by the non-profit organization The Peregrine Fund and the entire proceedings are available at http://www.peregrinefund.org/Lead_conference/. Other than a few color photos and figures online that are represented in grayscale in the print edition, there are no substantial differences between the book and the online version. The reader's personal preference is the best guide in deciding which version to acquire. Either way, acquire this book and spread the word! I strongly recommend this book to anyone who wants to be more knowledgeable about the threats to wildlife, humans, and the environment posed by the release of lead into our fields and wetlands.—JOHN CURNUTT, Regional Wildlife Ecologist, USDA, Forest Service, Eastern Region, 626 East Wisconsin Avenue, Milwaukee, WI 53203, USA; e-mail: jcurnutt@fs.fed.us

THE BIRDS OF THE REPUBLIC OF PANAMA. PART 5. GAZETTEER AND BIBLIOGRAPHY. By Deborah C. Siegel and Storrs L. Olson. Buteo Books, Shipman, Virginia, USA. 2008: 516 pages plus 1 inset map. ISBN: 978-0-931130-17-5. $45.00 (hardcover).—Even in these modern days of hand-held GPS receivers and Google Earth, the final volume of Alexander Wetmore's *magnum opus*: *The Birds of the Republic of Panama* is a welcome addition to the library of any serious student of neotropical birds who will want to make room for it along side the previous four volumes. It is outstanding in its primary role, as a 20th century ornithological gazetteer, but most modern readers will find it wanting a few 21st century trappings that were left out and we can hope will be included in some future format.

The authors, Deborah Siegel and Storrs Olson, have done meticulous work in providing geo-

graphic precision to ambiguous place names, which are the norm in much of Latin America. Those who have done field work in these parts are familiar with the simultaneous tendency for multiple local names for a single place, the application of a general name to a region too large to be considered a single biogeographic point, and the duplication of common names across distant districts and provinces. For example, this volume lists nine unique locations with the moniker "San José" which the authors dutifully sort out. Siegel and Olson have also been mindful of the tendency of place names to change, which is especially problematic for the areas surrounding the Panama Canal; in many cases, a Spanish-language place name replaced earlier English-language names used during the U.S. administration of the Canal Zone. I recently reviewed collecting localities for the *niglaris* subspecies of *Myrmeciza exsul* mentioned in *The Birds of Panama. Volume 3*. Not surprisingly I was able to find precise locations and geographical coordinates for all, but I should also note that I found the same information on Google; the value of this volume is in the annotations for each location. For example, many of the place name descriptions follow a hyperlink format, whereby other place names of interest relative to the location in question are referenced. It was in this way that I was able to make sense of the confusion surrounding Cerros Colorado, Santiago and Flores: an important endemic bird area in the Serranía de Tabascá in western Panama. It should also be noted the authors were careful with resolving the many unintentional variants of place names caused by collectors (including me) whose command of Spanish was less than perfect.

Equally valuable is the detailed annotated bibliography of Panamanian ornithology. The span of this bibliography is vast. Here, topics as diverse as systematics, paleozoography, and natural history comingle from both recent (up until ~ 2005) and historical sources. I am especially appreciative for the effort the authors undertook to include works not typically found in searchable data bases such as museum monographs and Latin American regional journals published in Spanish. This volume should foster the inclusion of these works into the cited literature of future studies. Particularly of interest is the inclusion of the reference for a multitude of named taxa (genus, species or subspecies) with a Panamanian type location; perhaps only the authors know how close to being an exhaustive list this may be.

Given this attention to detail, I wonder how much greater an impact this final volume – in what is largely a 20th century work – could have had if only more 21st century informatics were used. As an active collector of birds in Panama, one of my favorite features of the book is a map highlighting every collecting location (as well as the geographic gaps in our collective efforts). However, the map appears to be an afterthought, as it is a separate inset to the book. There is no way to go from a dot on the map to that place name in the text to learn more about who collected there and when. Similarly, there is no way to find all of the place names in any geographic region, such as the Pearl Islands or the Darién Province, despite how useful that would be. I imagine that many of my colleagues from the gene jockey cohort of ornithologists will appreciate the bibliography's detailed listing of 19th century taxonomic literature when it comes time to give proper names to resurrected lineages. However, without a searchable index for scientific names, I wonder if this resource will be used to its fullest capability. Providing a digital PDF of the text would allow for searching on strings such as province name or latitude and longitude ranges. Alternatively, perhaps the basics of the place names (and the point map) could be created as an internet-based resource; readers could be directed to the text for the details pertaining to specific locations. To be fair, other gazetteers of Latin American ornithology have these problems, but the fact that this volume was published in 2008 makes their omission more apparent.

It is worth noting the book begins with a short bibliography of Dr. Wetmore that includes his portrait and a detailed timeline of his field expeditions in Panama. This is fitting for the final volume of Wetmore's unparalleled work. Panama has had a much larger role in the development of neotropical ornithology than could be predicted by its geographic size. This is in no small part due to the generations of ornithologists that refer to well-thumbed pages of *The Birds of Panama* to learn detail after detail about the distribution and natural history of that country's birds. We are all indebted for his effort.—MATTHEW J. MILLER, Postdoctoral Fellow in Molecular Evolution, Smithsonian Tropical Research Institute, Apartado Postal 0843-03092 Panamá, República de Panamá; e-mail: millerma@si.edu

THE MIGRATION OF BIRDS: SEASONS ON THE WING. By Janice M. Hughes. Firefly Books, Buffalo, New York, USA. 2009: 208 pages, 76 color photographs, 27 maps and figures. ISBN: 13-978-1-55407-432-7. $40.00 (hardcover with jacket).—The biological study of migration, specifically among birds, is an extremely diverse field of endeavor. Over the past hundred years the literature is filled with diverse views and studies, each attempting to explain one particular facet of migration. The author of this work attempts to unify the great number of studies contributing to the understanding of migration.

The book is divided into six broad chapters, each with its own strengths and shortfalls–as to be expected in any attempt to cover such a complex topic. Ten "Profiles" are presented, two per chapter. These vignettes deal with specific species or groups of species that exhibit similar migration patterns or experience similar migration difficulties.

The opening chapter, "Bird Migration through Human History," was perhaps my personal favorite as it covered a great diversity of bird lore starting with mythological references, passing through classical references (such as Aristotle and Pliny the Elder) on to the treatise on falconry by the Holy Roman Emperor Frederick II in the 13th Century. At this point we start to see the origins of a more scientific study of birds that progresses to the present century.

The second chapter, "The Five Ws of Avian Migration," is the fuel for this amble through migration. It is here that the author introduces the reader to the varied aspects of bird migration. Researchers are occasionally and appropriately mentioned but there is a complete lack of reference citations. While this is undoubtedly a style preference for this type of book, citations would have made this a powerful chapter, instead of just an interesting one.

The third and fourth chapters, "The Phenomenon of Flight" and "Fueling the Migration," provide interesting aspects regarding the anatomy and energetic needs of birds. Again, citations would have been appreciated.

"Finding the Way," the fifth chapter meanders through the various ways that birds are believed to navigate. Here the reader is exposed to some classic experiments and studies in navigation. It is here that the anecdotal story of Cheri Ami should hold the reader on edge heading towards the ultimate chapter of the book. This World War I carrier pigeon (*Columba livia*) earned "the *Croix de Guerre*, one of the country's [France] highest honors for distinguished acts of heroism during combat."

The final chapter, "Migratory Birds in Peril," is really a one page overview followed by three birds with contemporary problems, a possibly extinct species (Eskimo Curlew [*Numenius borealis*]) and "An Indiscriminate Killer," which discusses the role of lighthouses and radio towers as man-made migratory hazards.

A glossary is a welcomed addition to any book of a highly specific nature. The one in this book covers the basic terms with which most non-scientists would need help. While it is quite brief, it is well done and should be of use to the casual reader. Following the glossary is a section entitled "Further Reading." This two page list of 33 books is inadequate for the topic, especially when considering three of the texts are reprints of Aristotle, Frederick II, and Pliny.

The writing throughout is well done and makes for enjoyable reading. The photographs are first-rate. This attractive combination draws the reader interested in migration deeper in, looking for more. But here it stops. The complete lack of references to the great number of studies that must have been consulted for this work will frustrate the reader in efforts to look elsewhere for greater detail.

While the author has attempted to cover the topic of migration thoroughly, I found it disturbing that Pliny the Elder garnered a citation in the index, whereas world-renowned migratory sites such as Point Pelee (Ontario), Whitefish Point (Michigan), Cape May (New Jersey), Malmo (Sweden), and Istanbul (Turkey), among others were lacking. This book is a cursory overview of a complex topic.

The appeal of this book will not be to the ornithological community due to the lack of referencing or detailed accounts of species or migration sites. It should, however, be in public libraries where it will have general audience appeal. Additionally, it will make a fine coffee-table book for the casual bird-watcher. Overall this book is best suited to middle school and high school libraries where young students will find it an interesting read, providing enough detail to stimulate interest. With adequate assistance, a student should be able to wade through the "Further Reading" section and continue on in studying the various aspects of migration.—MICHAEL A. KIELB, Visiting Lecturer,

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THE EASTERN SCREECH OWL: LIFE HISTORY, ECOLOGY, AND BEHAVIOR IN THE SUBURBS AND COUNTRYSIDE. By Frederick R. Gehlbach. Texas A&M University Press, College Station, Texas, USA. First Printing (1994). Second Printing (2008): 320 pages, 2 color, 36 black and white photos, 23 figures, and 27 tables. ISBN: (1994): 13-978-1-60344-121-6). ISBN (2008): 10-1-60344-121-2. $24.95 (paperback).—I highly recommend reading this study if there is anything at all you want to know or think you might want to know about screech-owls. There is little here that I can think of that might be gleaned from natural history observations that might have been left out. The text contains 10 chapters, 10 appendices, 297 notes, an index, and about 315 references. This is the story of serious field research and intimate contact with individual screech-owls, and with their populations in central Texas. It is a study spanning 41 years, that included 1,453 banded owls. The author involved homeowners, birders, school children, and teachers. It is a comparison of suburban versus nearby rural populations that were studied concurrently. The bulk of the study, reported in the first printing of this book (in 1994) was completed between 1976 and 1987. The (2008) printing contains new findings. Some things had changed: eggs are now laid 5 days earlier in the season than reported earlier. Wooded suburban habitat has decreased 26% due to suburban sprawl in the study plots, and nesting pairs have decreased 21% although their nesting success is still high.

In Chapter 1, the Introduction, Gehlbach tells us how, as a youngster, he was first introduced to screech-owls. He was riding his bicycle in a city park after a softball game when he saw three fledglings perched out of reach on a branch above him. He "knocked each bird off" (page 3) with a softball. Years later the mystery of the owls he had discovered that day remained in his memory as he encountered a pair nesting in a "squirrel box." (page 3). He soon made detailed observations and ended up putting up nest boxes and monitoring owls in several states (Ohio, New York, Michigan, New Mexico, Arizona, and also in Mexico). His close watch of the central Texas population that he reports started later, in 1967. In the Introduction, he outlines his study approach and methods of his statistical analyses. In Chapter 2, he delineates the climate and weather, and the vegetation of his study sites with correlates of the owls' choice of nest sites, as derived from nest boxes, as well as seasonal choice of roost sites. Chapters 3 and 4 examine food supplies and predation, and body weight and molt, respectively. The next three chapters concern details of nesting from eggs and chicks and their care to roles of males versus females during nesting. All of the data culminate in the last three chapters that concern lifetime reproduction and population structure, and comparisons of rural versus urban populations.

The wealth of detail is at times overwhelming, but each chapter has a summary page or two of 'The Essentials'. One can thus skim through the book to areas of individual interest and refer back to the detailed quantifications and statistics in each chapter. The coverage is far too wide and too detailed for me to reiterate in a review, and perhaps it should not be done, because everyone will find their own field of interest represented. As in any long-term study, the goal is to try to find repeating patterns. This is the exciting game of natural history, but there are also always unanticipated surprises that go beyond the original goals. Although the primary stated goal of this study was to compare rural versus suburban populations–and a number of significant differences were documented-for me the most fascinating discoveries were the unintended. To cherry-pick a few perhaps arbitrary examples, I was most intrigued by documentation of a 9-year population cycle, which coincides with a lunar periodicity, and occurred in both rural and suburban owls. It has apparently also been documented for diurnal birds. Other interesting nuggets were that life-long monogamy was the rule, but sequential and concurrent polygyny occurred when food was plentiful and nesting density high. The rufous phase declined more than the gray phase in hard winters but increased following rainy years. Birds were the primary vertebrate prey of these sit-and-wait predators, but insects and retiles were supplemental items. Blind snakes were taken into the nest as prey items but some survived in nests to live in a novel commensal association with the owls.

Gehlbach's three major conclusions, (pages 192-193) are: (1) the screech-owl is "especially well-suited to coexistence with humans". (2) "modern suburbia is quite munificent toward this

species... and [it] can utilize its resources'', and (3) ''the amenity-pre-adaptation connections certainly modify some ideas about avian ecology.'' Screech-owls are rather small owls and pre-adapted to live in the suburban environment as long as there are cavities and food that will satisfy a catholic diet. That said, the devil is, as almost always, in the details. And this book has plenty of them. As Gehlbach mentions himself (page 198): ''I have learned much and perhaps even more from Eastern Screech Owls [*Megascops asio*]; but long-term events like population cycles need more time...'' He continues to monitor the suburban population and writes (page 200): ''Field experiments are possible now that I know the rules of the game'' so the final phase of the investigation begins. He proposed that in the next few years he would use the owls in another study, in another city around a school curriculum to educate children (some of the owls were so habituated they would land on persons and one could reach under them to take eggs and chicks to examine and measure without disturbing the birds). These owls are an excellent study animal for children and the public to get familiar with wildlife, and through his birds he hopes to continue to promote an urban blend of nature and culture. Gehlbach's practical directions for future comparative studies will raise awareness and help promote the provision of habitat and nesting sites for these charismatic birds, which are a barometer of some aspects of the urban environment.—BERND HEINRICH, Department of Biology, University of Vermont, Burlington, VT 05401, USA; e-mail: bernd.heinrich@uvm.edu

BIRDS OF EAST ASIA: CHINA, TAIWAN, KOREA, JAPAN, AND RUSSIA. By Mark Brazil. Princeton University Press, Princeton, New Jersey, USA. 2009: 528 pages, 236 color plates, 2 pages line drawings, 2 maps, 950 distribution maps, family key, 2 appendices, index. ISBN: 978-0-691-13926-5. $39.95 (paper); ISBN: 978-0-691-13925-8. $79.50 (cloth).—When I first visited Japan, Korea, and Hong Kong in 1960 aboard the USS Helena (a heavy cruiser) as a freshly minted ensign in the U.S. Navy, there were no field guides covering any part of Asia. My only guide to the area was Keisuke Kobayashi's ''*Birds of Japan in Natural Colors.*'' Although helpful because of its excellent illustrations, it was difficult to use as the text was in Japanese. Over the ensuing years, numerous books on the birds of eastern Asia were published, including guides to the birds of China, Taiwan, Japan, and Korea (but none for northeastern Russia). All of these books are useful and expand the knowledge of the birds in those areas. However, each has their drawbacks, one of the main ones being that they treat only the birds already known to have been found in the area covered. The gap that remained was a modern field guide that tied all of these areas together in a broad overview.

This new guide fills that void very well. It covers all the birds known to have occurred in northeastern Asia roughly east of longitude 116° E, thus all the coastal Chinese provinces north from Fujian (opposite Taiwan) to the Arctic Ocean and east to the Bering Sea, including northeastern Russia, Japan, Korea, Taiwan, and their satellite islands. Further, it is a competently executed field identification guide lavishly illustrated in the modern fashion with the text for each species facing its plate.

The use of ''East'' Asia in the title is both misleading and inaccurate as the guide is concerned only with ''northeastern'' Asia. None of southeastern Asia is covered. The brief introduction of 8 pages contains: Aims of this guide, Geographical scope, Taxonomy, Nomenclature, Bird identification, Bird habitats, Migration, Vagrancy, and How to use this book (which includes 2 pages of line drawings illustrating avian topography and terminology). This is followed by a 16-page key to the families with a color thumbnail portrait of a representative species from each family. The brief text for each family discusses general habits of the family members which will help place an unidentified bird in its family.

The bibliography lists only 16 titles. Since a work such as this requires use of hundreds of references, listing only a few seems pointless. However, the entire reference list (and other information about the book) can be found at: http://sites.google.com/site/birdsofeastasia. Appendix 1 is a useful table giving the status in five broad areas (Chinese coastal and northeastern provinces, Taiwan, Korea, Japan, and northeastern Russia) of each of the species recorded in those areas. Appendix 2 is a list of 46 species considered likely to occur eventually in northeastern Asia.

All 969 species known to have occurred in northeastern Asia are illustrated in color paintings on 236 color plates. An additional 16 species that are expected to turn up are illustrated in the plates,

as well as eight extinct species. Each plate displays 2–8 species with 1–11 images/species. The entire text for each species is opposite its plate and consists of a small (2.2 × 2.1 cm) range map in seven colors, length, wingspan and weight, distribution, habitat and habits, identification, bare parts, and vocalizations. Some have taxonomic notes or alternate English names. On the same line with the title 'English name' is a useful code indicating in which of the five geographical areas covered the bird has occurred. By using tiny print, a large amount of information was crammed into the text for each species. However, for some complex groups such as large gulls and diurnal birds of prey, the book's format is crippling as it does not allow a sufficiently long text. The taxonomy throughout is up to date and forward-looking.

The color plates were executed by 14 artists, resulting in uneven quality, most in the good to very good level with some in the excellent to superb range. With only a few exceptions, their goal of enabling identification is attained. Females and immatures are illustrated where they differ from the adult male, as are the more different subspecies, offering mostly complete coverage of plumage variation. All individual images are identified by age, male or female, and often subspecies. Where identification characteristics are revealed only or best in flight, inserts of birds in flight are given. The artists responsible for each plate are listed only in the copyrights section on the backside of the title page. I believe the name of the artist responsible for each plate should be displayed prominently either on the plate itself or on its facing page. Some of the plates I found most satisfying are: Alan Harris's diurnal raptors, Brian Small's bush-warblers through *Acrocephalus* warblers, and Ren Hathaway's large thrushes. I am uncomfortable with the brush strokes in many of Dave Nurney's birds, as well as the odd postures and proportions and too-large heads of some of his birds. Some comments by plate follow.

Plate 22. While the text correctly notes the crown and nape of the adult Pacific Loon (Diver) (*Gavia pacifica*) is noticeably paler than the Black-throated Loon (Diver) (*G. arctica*), the plate has this reversed and the difference diminished, likely due to using specimens rather than field experience, as the contrast is accentuated in the brighter light in the field.

Plate 41. The underwing pattern of both adult and immature Spot-billed Pelican (*Pelecanus philippensis*) is inaccurate. It should have a rather banded appearance with white greater and median underwing coverts contrasting with vinous (adult) or dusky brown (immature) lesser underwing coverts and dusky brown (looking paler or darker depending on light angle) primaries and secondaries. The outer primaries are blackish.

Plate 46. Adult and immature labels are switched on Eastern Osprey (*Pandion cristatus*).

Plate 48. I had the privilege of seeing an adult of the "*niger*" subspecies (or morph) of Steller's Sea Eagle (*Haliaeetus pelagicus*) in South Korea on 3 January 1962 and aver this entirely black eagle with its huge yellow bill and white tail could not possibly be mistaken for anything else, contra the text.

Plate 52. While the crest of the Crested Goshawk (*Accipiter trivirgatus*) in the wind could possibly look like the plate rendition, it normally lies flat on the nape with the tip slightly above the nape (perhaps 2 mm.) and just barely visible.

Plate 54. The complexity of the plumages of the buzzards (*Buteo*) can only be hinted at in the space available here, e.g., the individual tail feathers of most Upland Buzzards (*B. hemilasius*) are white in the center and darker on the edges so that the tail looks mostly white when spread and darker when closed.

Plate 59. While the flight picture of Ruddy-breasted Crake (*Porzana fusca*) accurately depicts this bird's "jizz", the walking bird is both badly misshapen and too large (should be smaller than Band-bellied Crake [*P. paykullii*]).

Plate 65. The specific name of European Golden Plover (*Pluvialis apricaria*) is misspelled (*aricaria* rather than *apricaria*).

Plate 69. Neither mentioned in the text nor pictured properly is the fact the white flank feathers of the Greater Painted Snipe (*Rostratula benghalensis*) in flight curve up and over the sides of the base of the tail to give a distinctive Ruff-like pattern.

Plate 71. The width of the white band on the tips of the secondaries of the Common Snipe (*Gallinago gallinago*) and Wilson's Snipe (*G. delicata*) are different and incorrectly depicted (switched) in the plate (correct in text).

Plate 90. Missing in text is the fact that Relict Gull (*Ichthyaetus relictus*) often forages along shore like a shorebird.

Plate 104. The Marbled Murrelet (*Brachyramphus marmoratus*) is pictured and listed as a species that might turn up in northeastern Asia. However, there is a record for Idlidlya Island in

Koluchia Bay on the northern Chukotka Peninsula (Dement'ev et al. 1951, *Birds of the Soviet Union*).

Plate 115. Eastern Grass Owl (*Tyto longimembris*) text and plates depict only buffy phase. White phase has white underparts and white upperside of tail with narrow black bars.

Plate 120. The text account of Brown Hawk-Owl (*Ninox scutulata*) is a bit muddled. My 2002 paper (Bulletin B.O.C. 122: 250–257) on this species complex showed the song of the migratory northern race *japonica* is the same throughout its range and different from the resident races in southern Asia. I recommended splitting them based on vocalizations as well as some morphometric differences. The resident subspecies *totogo* (southern Japan and Taiwan) is close to *japonica* both vocally and morphometrically with a weak potential for a split. Brazil chose to split the *japonica* subspecies into eastern *japonica* and western *florensis* and suggests that only *japonica* might be separate from *scutulata*, which doesn't make sense (*japonica* and *florensis* have identical vocalizations and similar morphometrics, which are consistently distinct from the subspecies of *scutulata*). The English name I suggested in my paper, Northern Boobook, is mentioned, but the paper is not listed in the online bibliography.

Plates 127, 130. The colors of Rufous (*Celeus brachyurus*), Pale-headed (*Gecinulus grantia*), and Bay (*Blythipicus pyrrhotis*) woodpeckers are very badly off.

Plate 133. Heads of Tiger Shrikes (*Lanius tigrinus*) are much too big.

It should be noted that any new work with as broad a sweep as this one, and its consequent massive number of data points, inevitably has short-comings. That this one has so few is a tribute to the care and expertise applied to the project by the author. It is remarkable indeed that the book is so far along the route to perfection on its first try.

This guide covers its area quite thoroughly, enough so, that I would be quite comfortable carrying it as my only guide in its geographic range. Further, it will be quite useful in the Philippines and Indonesia. Birders throughout Eurasia and North America will find it helpful for identifying strays. I highly recommend this book to anyone interested in Asian birds and expect to be using it in my Asian jaunts.—BEN F. KING, Ornithology Department, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA; e-mail: kingbirdtours@earthlink.net

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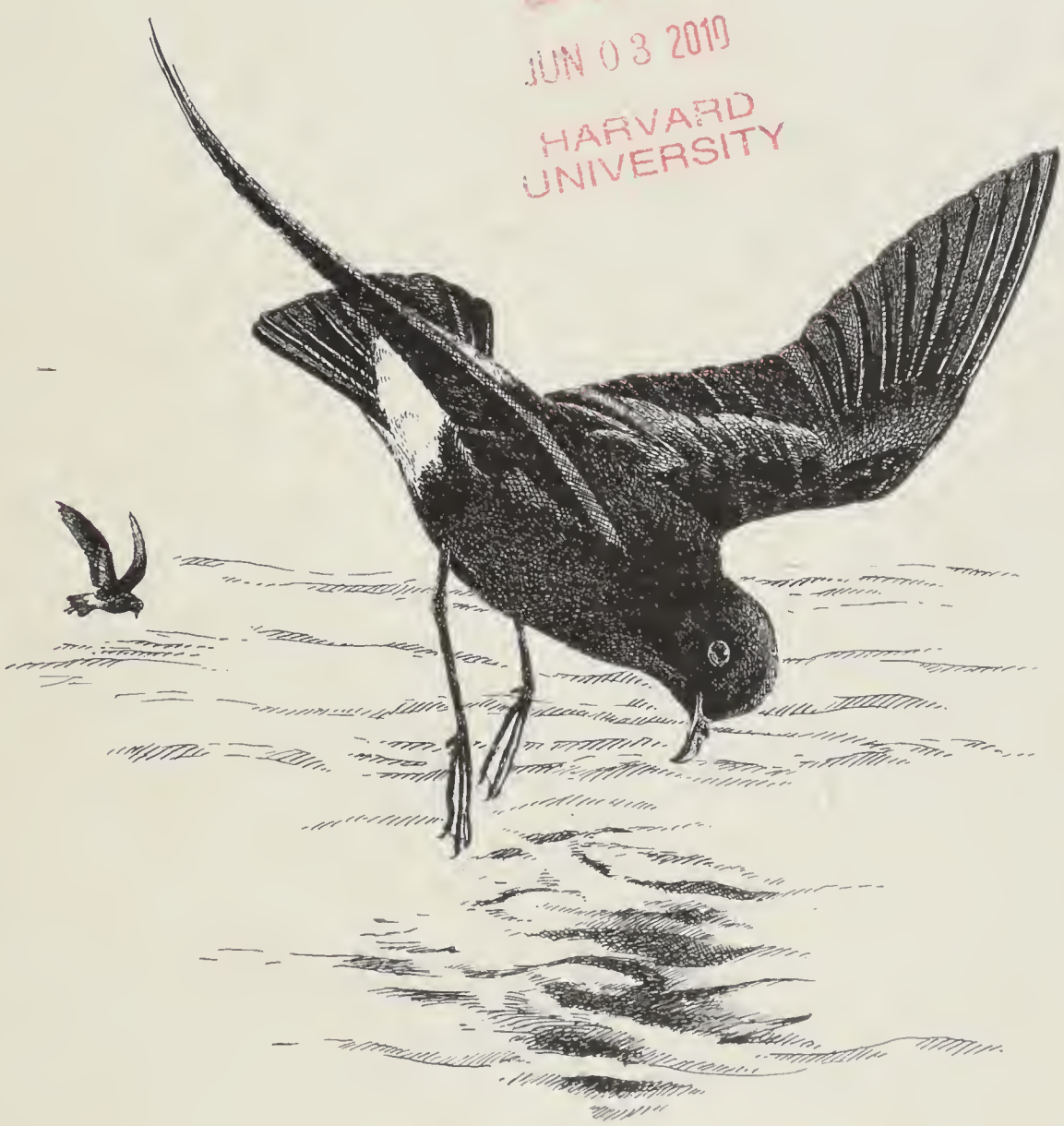

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COVER: Wilson's Storm Petrel (*Oceanites oceanicus*). Illustration by Don Radovich.

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FRONTISPIECE. We quantified male and female parental care by House Sparrows (*Passer domesticus*) to ascertain food provisioning rates by each parent (page 211) during the 2-week nestling period. Adult fitness was shaped primarily by the parents' ability to deliver enormous insect prey items to offspring. Parental success (i.e., total recruitment of offspring) was predicted by size and numbers of offspring at banding (day 11). Water color by Don Radovich.

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NOT THE NICE SPARROW
The 2007 Margaret Morse Nice Lecture

DOUGLAS W. MOCK[1,2] AND P. L. SCHWAGMEYER[1]

ABSTRACT.—We began our studies of House Sparrow (*Passer domesticus*) biparental care in the mid-1990s by applying the classic Margaret Morse Nice field technique of color-banding individuals. Over the ensuing summers, we slowly accumulated quantitative provisioning records for 100 broods, even as we commenced a series of experimental manipulations. Provisioning data showed parental fitness, as expressed by offspring recruitment into the local breeding population, to be shaped mainly by the adults' ability to deliver enormous insect prey items. It also turned out that production of robust and competitive fledglings routinely involves losing one or more nestlings (brood reduction in 42% of 1,000 multi-chick families). Recruitment success was compensated for the death of an offspring if the subsequent reallocation of food enables surviving nest-mates to gain at least 2 g more before fledging. Video samples showed that parents of day 3 broods favored larger siblings, even though brood reduction typically occurs on ~day 4, suggesting that adults participate actively in promoting some offspring over others. The social dynamic affecting how parents work as a team during provisioning does not fit the pattern expected if partners negotiate actively with one another, but points more toward the likelihood of "sealed bids." Specifically, experimental handicapping of individual parents (tail-weights and hormone implants) indicates partners operate quite independently during brood-rearing. We are now extending our experiments into the incubation phase, where parents are probably better-informed about partner activities, thus potentially able to adjust to fluctuating contributions. Finally, behavioral rules affecting food deliveries seem to differ for females and males. Females normally increase provisioning as the brood ages, but males do not. However, when broods received supplemental nutrients, males matched the female upsurge, accelerating their deliveries by 25%, showing they usually work well below capacity. *Received 31 December 2009. Accepted 28 February 2010.*

Among the many contributions for which bird behaviorists are grateful to Margaret Morse Nice, her pioneering use of color bands is probably the most universal. Color-banding seems utterly fundamental to behavioral ornithologists today—a trifle really—but on 26 March 1928, one pink celluloid ring provided Mrs. Nice with a means of recognizing a particular male Song Sparrow (*Melospiza melodia*) near her Columbus, Ohio home. Soon she banded a second male with a green ring, thereby exposing consistent differences between the two in song, aggressiveness, etc. It is hard to overstate what a difference this innovation has made to behavioral field studies.

Pausing to think about it, much that we take for granted today was not available to Margaret Nice. For example, well before today's ornithological neophyte affixes any color bands, the step of identifying the local avifauna, or even finding out which birds live nearby, promotes a trip to the

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bookshelf for a field guide where the only dilemma is which one to choose. When Margaret Morse Nice arrived in Oklahoma in 1913 (her husband Blaine had been hired in what is now the Zoology Department where we both work), no bird guides or even checklists existed. Although she had strong academic credentials (including a Master's degree from Clark University), she never held a position at the University of Oklahoma. Instead, she stayed physically busy with the traditional duties of wife and mother, while fighting boredom and intellectual frustration by reviving her ornithological interests. Eventually she wrote Oklahoma's first state bird book but, by the time it was published, the family had moved (with Blaine's career) to Ohio State, where she began to focus on avian behavior.

The Oklahoma house that Blaine Nice built (literally!) at 445 College Avenue is just a block from where we now live, but nearly everything else has changed. The streets have been paved, more than one faculty member owns an automobile (indeed, it seems as if most OU students have more than one!), and women now comprise a third of our department's faculty. Meanwhile, Margaret Nice's fields of natural history and ethology have been infused with theoretical and mathematical fibers to form modern behavioral ecology (Parker 2006). We all inhabit this new world, but should pause from time to time and acknowledge the extraordinary spadework that made our studies possible.

That said, many Nice-era roots remain clearly visible, despite being taken for granted. House Sparrows (*Passer domesticus*) were already abundant in Norman when she arrived in 1913, but we have now color-banded several thousand since 1994. Otherwise, we spend much of our field time sitting quietly and, hopefully, recording what the birds would have done in our absence.

The overarching goal of our collaborative research program is to understand what makes biparental care evolutionarily stable. Because cooperation in parenting makes a major contribution to social monogamy, which predominates in Class Aves, we see it as central to understanding that mating system. House Sparrows are abundant and willing to use nest boxes, so we study House Sparrows. This also is consistent with the Margaret Morse Nice tradition of studying "... what appeared common to so many" (Nice 1979:263).

We thank the Wilson Ornithological Society for honoring us with the 2007 Margaret Morse Nice Medal and offer the following sketch of some things we have learned about these quintessentially ordinary birds through a series of shared projects. Our goal is not any sort of autobiographical detail, except as it relates to the evolution of our sparrow research program, but to provide an overview of several related studies that have led us to our current work. We do not presume to offer this account as a model of how anyone else should proceed, but students of bird research need not regard the whole field process as mysterious. To reduce that mystery, we explain how we try to extract our guiding questions from the general picture, use them to design empirical exercises, and then seek to re-apply the analyzed results back to the bigger issue from whence we start. Along the way, it must be confessed, we often stumble. Space limitation and reader interest preclude a full chronicling of all our mistakes (trap designs that were prone to equipment malfunctions, an attempt to supplement breeding parents with live mealworms that escaped, occasional duplications of color band combinations, etc.), but we hope students will forgive themselves for similar false starts as they press forward.

We both came of age as scientists more or less as Darwin's theory of sexual selection was being revived after a century of neglect (Campbell 1972) and as several other major pieces of the evolutionary puzzle, especially inclusive fitness theory (Hamilton 1964a, b) and optimality modeling (reviewed in Parker and Maynard Smith 1990), were coming into focus as the foundations of behavioral ecology. Unlike some previous awardees of the Margaret Morse Nice Medal, we had not grown up as bird-watchers per se, but more generally as animal enthusiasts. Knowing from childhood that we wanted to have "animals" in our lives, we had gravitated naturally toward animal behavior research while in school. Arriving independently 2 years apart and meeting for the first time as University of Oklahoma faculty members, we continued with our separate lines of study for quite a few years focusing on scramble-competition polygyny and sperm competition in local ground squirrels (e.g., Schwagmeyer 1988, Foltz and Schwagmeyer 1989, Schwagmeyer and Foltz 1990), and fatal sibling rivalry and parent-offspring conflict in egrets (e.g., Mock 1984, 1985; Mock et al. 1987). Realizing that we needed to learn more about mathematical modeling, we visited several British universities over the 1983

Christmas break, pausing to get married in Edinburgh. It was easy to agree on Geoffrey Parker as our theoretical mentor and collaborator, as he had discovered sperm competition (e.g., Parker 1970) was having a major role in the development of Evolutionary Game Theory (e.g., Maynard Smith and Parker 1976, Parker and Stuart 1976, Parker 1978, Parker 1983, Parker and Maynard Smith 1990), and was already deeply involved in modeling both of our research topics (e.g., Parker and Macnair 1978; Parker 1982, 1985). We spent fall semester 1984 with him at the University of Liverpool, taking turns working on models with Geoff and spending the rest of our time either pulling numbers out of squirrel and egret data sets or desperately salvaging our neglected mathematical training. Over the ensuing years, we produced two separate series of publications with Geoff (e.g., Schwagmeyer and Parker 1987, 1990; Parker et al. 1989; Mock and Parker 1986, 1997), then began searching for a field system to explore together. That led first to two field seasons working on Glaucous-winged Gulls (*Larus glaucescens*) in Puget Sound, specifically on their pre-hatching acoustic communications (Schwagmeyer et al. 1991), before we decided to focus on biparental care in House Sparrows.

CHOICE OF PROBLEM

Biparental care and monogamy are not superficially sexy topics, at least on the surface. Except for feathered vertebrates, both traits are exceedingly rare in nature. Thus, the question naturally arises: what ecological and evolutionary forces generally promote the evolutionary stability of reproductive cooperation between two adults? Why have birds, in particular, adopted these as the norm, when other taxa have not? Finally, although many human cultures (including our own) claim both as societal goals, why are they so elusive? It seems logical to explore the underlying problems of shared parental care (seeking what may be broadly general causes) by analyzing the behavioral dynamics with birds. Furthermore, it makes sense to choose a bird that is common and amenable to (non-destructive) experimental manipulation of the targeted behavioral components.

Biparental investment is most simply explained as the pattern that emerges when neither of the sexual partners has anything better to do with its time. Specifically, if either parent has the realistic option of alternative pursuits that deliver higher average fitness returns, those distractions would likely undermine the joint endeavor (Maynard Smith 1977). Understanding the fitness payoffs available to each "player" for its various alternatives lies at the heart of the matter. In many taxa (e.g., mammals and plants), dependent offspring remain physically anchored to the female, extracting nutrients from her for extended periods. This arrangement "emancipates" the other parent to explore additional potential reproductive opportunities. Similarly, when offspring are not physically attached, and especially when their basic requirements are lessened (e.g., by precocial development), it is easy to see how uniparental care may suffice across a broader array of taxa. If low-cost offspring are shed soon after fertilization, the uniparent is less rigidly pre-ordained and "sex-role reversal" is more easily evolved (males serving as solo care-givers in many fishes and shorebirds, for example). In most birds, combining of egg-laying with altricial development seems to have created a middle zone in which more than one adult can make valuable contributions to offspring welfare. In short, when each embryo is placed in a neutral arena (nest) soon after it has been fertilized—and especially if a hasty departure by the first male reduces the chance that his sperm will fertilize the next ovum—the male has inducements for sticking around at least through the laying period. Thereafter, if he can further his own selfish interests better by providing additional services to his offspring (directly to the eggs and/or by proxy to his partner), than by seeking additional mating opportunities, he may remain. Once hatching begins, the need for provisioning with vast quantities of exogenous food can extend male participation on the home front (along with the continuing parental tasks of defense against weather and enemies, etc.).

Following this argument, ecological and phylogenetic circumstances may provide plausible reasons why biparental care is evolutionarily stable across ~90% of feathered vertebrates (Lack 1968, Clutton-Brock 1991), yet rare in all other life forms. Parental duties seem sufficiently extensive to require a team of care-givers and, perhaps equally important, to preclude either the option of dumping the whole brood-rearing exercise on the other (i.e., the "cruel bind" of Trivers 1972), lest the abandoned parent simply follow suit and allow the brood to fail.

To put a face on the overall dynamic, consider House Sparrow reproduction. After ~11 days of incubation (some by the male), four or five hatchlings emerge that will develop from tiny (1–2 g) naked ectotherms into fully feathered, warm-blooded, adult-sized (20–25 g) flying machines within just 2 weeks. During the nestling period, the two adults must find, capture, and deliver (typically one per trip) 3,000 to 4,000 unwilling insects to fuel this growth. At the same time, the parents also provide brooding warmth (at night and on chilly days), resist certain predators (and various other intruders, including hostile conspecifics), and maintain a modicum of nest sanitation by removing fecal sacs. Although most House Sparrows are socially monogamous, some males acquire two partners simultaneously and many females accept gametes from extra-pair males: in our Oklahoma population, ~17–20% of young are sired by other males (and 41–45% of broods contain one or more such extra-pair offspring) (Whitekiller et al. 2000, Edly-Wright et al. 2007). Overall, these are pretty ordinary passerines and, thus, a useful model system.

CHOICE OF SUBJECTS

According to W. L. Dawson (1903:40), "Without question the most deplorable event in the history of American ornithology was the introduction of the English Sparrow." We may wince over that sweeping indictment, hastily noting that the arrival of European hominids was surely more "deplorable" for native bird species by virtue of myriad associated ecological nightmares (e.g., novel pathogens, deforestation, pollution, and introductions of numerous destructive exotics, especially pets, livestock, and all the birds mentioned in Shakespeare, etc.), but we get Dawson's point: this is not the most glamorous and beloved bird in the New World. We did not pick it for glamour. As behavioral ecologists, we chose our topic first and then sought the best local bird with which to pursue it. Had bluebirds, chickadees, or wrens piled into our nest boxes, we might well have studied them. But we were expecting sparrows and chose two sparsely occupied (by humans), university-owned tracts near campus for our study areas, partly because many House Sparrows were already nesting in the porous old buildings left from a World War II naval air station. One of these decaying structures is still dignified as the university's Animal Behavior Laboratory. Our goal was to lure sparrows from those decrepit buildings to fine, new nest boxes mounted where we could reach them conveniently. Surveying possible box designs, we learned that standard bluebird houses are annoyingly popular with House Sparrows and explicit warnings advised us that House Sparrows like having a perch, prefer being near human-occupied buildings, etc. We actively catered to sparrow tastes. In the early seasons, we had problems with a few avian predators, particularly Loggerhead Shrikes (*Lanius ludovicianus*) that trap-lined our boxes, harvesting sparrow nestlings simply by sticking their heads through the hole and seizing the tallest beggars. To thwart this, we attached a simple 10-cm long corridor of galvanized hardware cloth to every box. The sparrows did not mind entering through these hall-like structures and mass-predation losses dropped.

TRAPPING, MARKING, AND CENSUSING

We used the usual trapping methods for building a color-banded population, including walk-in traps baited with seed and bread, mist nets, and even sneaking up on brooding males to catch them in nest boxes. We learned the hard way not to touch desertion-prone females during incubation. We applied three color bands (slitting toy Perler Beads as an inexpensive supply; Hill 1992) and one aluminum band in unique combinations for each bird. After much trial-and-error with a variety of in-box trap designs, we developed a Rube Goldberg contraption involving a modified wire corridor (sporting a drop-down door to prevent exit), some monofilament fishing line, a rat-trap, and remote-control toy car electronics that empowered us to catch uncooperative individual adults during their brief visits to provision chicks (Mock et al. 1997). The general problem was that House Sparrows are smart and wary: catching one member of a pair without disturbing its mate required a trap that was simultaneously invisible, under our instantaneous control from considerable distances, and impervious to strong prairie winds. Once captured, we carried subjects inside an opaque bag to a car, processed it there (weighing, banding, etc.), and then carried it to some stranger's vehicle for release: simply releasing it from one's own car was found to lead to scolding of that vehicle during subsequent attempts to observe behavior.

BEHAVIORAL SAMPLING

Reliable quantification of male and female parental care took advance preparation to opti-

mize the later research effort. A chief goal was to ascertain food provisioning rates by each parent (Frontispiece) across the 2-week nestling period. We needed a sampling regime that would generate representative estimates. Average figures in quite a few published field studies of avian parental care are based on rather scant samples (at times just 15–30 min observations taken on 1–2 days convenient to the researchers) without any attention given to whether these capture the essence of the parents' activities across daylight hours, age of the nestlings, shifts in food availability within and between seasons, etc. Because we were going to do a lot of monitoring over several summers, we wanted to know how much sampling was needed and when this should be done. For this purpose, we conducted a preliminary study in which we recorded parental delivery rates intensively at five nests (covering all daylight hours and brood ages), then performed regressions on these over-sized samples to see if some times of day (and/or combinations thereof) captured most of the variation. We learned that a single hour-long sample taken mid-day yielded a good picture of the whole day's provisioning (between-nest comparison), but one taken in mid-morning did the worst (see Schwagmeyer and Mock 1997 for details). Combining samples delivered 91–99.7% (depending on which hours) of the variation between nests and nearly 80% of within-nest variation. In the seasons that followed, we used these findings to guide our deployments, eventually amassing parenting records for more than 100 broods based on >13 of these selected hours per brood. During these observations, we recorded parents' arrivals and departures, size of prey being carried (three categories, scaled against adult beak), and other activities performed near the nest (e.g., foraging, singing, defending, etc.) These data provided a good picture of parental care in regular sparrow nesting cycles and in those subjected to experimental manipulations.

BUILDING SUCCESSFUL OFFSPRING

At the heart of any parental care problem lies the question of what is needed to produce valuable offspring. There are many components, including protection from the elements and predators, but finding and delivering sufficient food to the brood (provisioning) and then distributing it optimally once home (allocating) are generally assumed to supersede most other concerns, because of the phenomenal growth challenge of offspring. Once eggs have hatched, parentally delivered food is the chief factor limiting growth, survival to fledging, and recruitment to breeding age of House Sparrow offspring; hence it is a major determinant of parental fitness. Provisioning, as the central task shared between the parents, was the initial focus of our exploration into the stability of biparental care.

If food is limiting, the simplest prediction is that offspring growth and survival should be density (brood-size) dependent for a given level of parental effort. This is usually assessed over the short span of the nestling period (volant offspring being necessarily harder to count) as one discrete exercise. In many field studies, brood size at hatching is compared with survival and body mass at fledging (typically defined as banding age, just before first flight). This requires only a brief census visit at hatching and measurement of body size during the banding process. Few field studies calibrate those relationships with intensive sampling of actual food delivered, presumably because this feature is tedious and time-consuming. A separate exercise, seldom performed in tandem with pre-fledging evaluation, extends the matter from that point by comparing how fledging production (e.g., size and numbers of banded chicks) translates into offspring survival to breeding age. This second step has produced far greater documentation (for at least 22 avian species; reviewed by Magrath 1991, Schwagmeyer and Mock 2008) of the commonsense idea that parents producing more and larger fledglings should consequently achieve greater recruitment of breeding offspring.

We were committed to doing the necessary observations of provisioning, as an essential part of analyzing biparental division of labor, and took the opportunity to combine the two steps (pre-fledging and post-fledging) on the marked House Sparrow population. Mean offspring mass on day 11, to our mild initial surprise, was not predicted by total food deliveries, but was strongly predicted by the rate at which the "enormous" category of insects (>2 cm total body length, hereafter, "e-prey") were provided (Schwagmeyer and Mock 2008). Once a correction is made for the much greater volume and mass of e-prey, it seems likely these grasshoppers, caterpillars, etc. can provide most of the nutrition early in the season, despite being relatively uncommon (~14% of all deliveries). Thus, total amount of

food is important, as expected, but simple counts of parental food trips—as might be recorded by automated devices—would have pointed to the opposite conclusion.

We used reobservations of 100 banded offspring from a sample of 1,028 broods to evaluate how chick numbers and mean mass relate to local recruitment. This measure of parental success was predicted by both size and numbers of offspring at banding (Schwagmeyer and Mock 2008).

We found that our data from 99 broods observed for provisioning rates were sufficient for a direct assessment of how food deliveries affect recruitment. This connection had been established before only once, for Long-tailed Bushtits (*Aegithalos caudatus*), a cooperatively-breeding British bird (MacColl and Hatchwell 2003). Total delivery counts once again failed to predict survival to breeding age in our sparrows, but e-prey deliveries did (Schwagmeyer and Mock 2008). Overall, it seems clear that e-prey availability is a key determinant of parental success and these food items have an especially strong effect on recruiting for earlier broods.

Considering that parents presumably cannot simultaneously maximize both the number and sizes of current brood members, much attention has been given over the years to short-term adjustments they may make during the period of offspring dependency. Early mortality of individual nestlings has the potential to relax competition for insufficient food and the idea that brood reduction might be engineered by parents as part of an adaptive strategy for tracking unpredictable food availability dates to the classic writings of David Lack (1947, 1954). The resolution of acute sibling rivalry in some taxa includes extreme forms of nestling aggressiveness and even specialized weaponry, but in many it results from low-key processes of scramble competition (reviewed in Mock and Parker 1997). Passerine brood reduction falls overwhelmingly into the latter category and it is hard to learn unambiguously whether the loss of any given brood member makes a positive contribution to the inclusive fitness interests of surviving parents and siblings, an overall negative, or a matter of little importance one way or the other (O'Connor 1978).

We found that 42% of 1,000 multi-chick House Sparrow broods experienced partial-brood mortality between hatching and fledging (Mock et al. 2009) with greater frequency in larger broods, as one would expect. Most of these losses occurred early in the nestling period (median day 4), before parental capacities to provision are likely to be overtaxed. We found parental provisioning (in the closely observed sample) increased from broods of three to broods of five, and per-capita food remained relatively even. Family size was a strong predictor of whether brood reduction occurred (provisioning and family size are both good predictors of the proportion of the brood surviving to fledge). Once a single-chick mortality event had occurred, parents did not trim their provisioning rate, as has been documented for siblicidal Cattle Egrets (*Bubulcus ibis*; Mock and Lamey 1991) and Brown Pelicans (*Pelecanus occidentalis*; Ploger 1997); thus, sparrow survivors tended to receive a food bonus in the aftermath of brood reduction.

We took two further steps to explore whether parents might favor or disfavor brood reduction. We affixed tiny video cameras above false ceilings inside 11 nest boxes containing broods of four and recorded how food was distributed when nestlings were sufficiently young (3 days) that allocation could be attributed safely to parental decisions (i.e., not to nest-mates' jockeying effectively for positional advantage). The idea was to see if fully empowered parents show overt favoritism toward the smallest chick(s) in each brood by giving runts more food. These parents skewed allocation more to larger chicks (Mock et al. 2009), a pattern that persists (and often increases) after the stronger chicks usurp increasing control over allocations. Thus, brood reduction victims tend to be those that were smallest initially. Second, we analyzed the trade-off between size and numbers of fledglings on recruitment to estimate how much additional body mass of surviving nest-mates is required to compensate parental fitness for loss of one offspring. This exercise suggested that one chick's death is fully reimbursed if its surviving siblings fledge about 2 g heavier (e.g., by virtue of the food the victim would have consumed). Beneficial reallocation probably occurs often, apparently when parental control is at its peak (Mock et al. 2009).

The foraging task shared between two sparrow parents is something of a malleable abstraction, perhaps roughly estimated (within a range of limits) when clutch size is first known to both partners, but then shifting over the course of events including hatching failure, seasonal ebb and flow of food availability (insect hatches,

periods of inclement weather, etc.), and loss of nestlings.

DO PARENTS NEGOTIATE WITH EACH OTHER?

The most influential hypothesis for biparental cooperation outlines a behavioral dynamic between two monogamous partners as being the fruit of a negotiation (Chase 1980, Houston and Davies 1985, McNamara et al. 1999). This assumes that each parent has a generally self-serving level at which it is willing to work, but must coordinate with a like-minded partner. The "self-serving" qualifier reflects that participants are not genetic kin, so their confederation is held together by personal fitness interests (*cf.* inclusive fitness incentives). Each individual seeks the best deal possible, despite needing a sexual partner, within the framework of its joint reproductive enterprise, while prefering that its partner provide somewhat more than half of the work. Both partners cannot realize this preference simultaneously. Just as union representatives and owners engage in a series of offers and counter-offers during a labor dispute (Maynard Smith 1982), male and female parents are envisioned as adjusting and readjusting their levels of effort, either in evolutionary time or in real time, until each is satisfied that it cannot get a better deal. This final pair of positions is, in the parlance of evolutionary game theory, the ESS (Evolutionarily Stable Strategy) solution.

One attractive feature of this Negotiation Model for biparental care is its testable prediction of *partial compensation*, the optimal response that a parent should make if its partner seems to do less than its share. For illustration purposes, imagine that an idealized pair has a clean 50-50 split of the family-raising labor, then the male starts gold-bricking by cutting his share down to 30% of the total, leaving a 20% shortfall. The model reasons the female should not compensate fully (by making up the whole difference), but take up only part of the slack. If the system is working properly, the male's interest in offspring welfare should prompt him to increase his contributions (whereupon she decreases, etc.) until equilibrium occurs.

Field tests of the Negotiation Model had begun to appear in print as we were starting our sparrow project. The basic experimental approach involves unilateral handicapping, that is imposing a burden on one partner to reduce its contributions and simulating "gold-bricking." With one parent slowed, the unencumbered partner's behavior is monitored to see if it provides partial compensation (vs. full compensation or even no compensation, etc.). We followed the example of Wright and Cuthill (1989) in crimping four small lead split-shot fishing weights onto the rectrices of the handicapped parent (male or female), loading ~5–7% of total body mass away from its center of gravity. After finding that some birds in the first season had lost these weights, we painted them with red nail polish in later years, enabling us to confirm retention through spotting scopes. Limiting our study pairs to those with clutches of either four or five eggs, we rotated among the experimental and control treatments (minimizing season effects). Our routine was to sample pretreatment provisioning behavior for a total of ~5 hrs prior to treatment (typically by day 5 posthatching) and to collect another 9–10 hrs of data after treatment.

Females in control (unmanipulated) pairs typically increased provisioning throughout the nestling period, while males leveled off after about the fifth day (Mock et al. 2005). Our experimental treatments showed unexpected responses. When males were handicapped, they had only a slight decrease in mean delivery rate, but they reduced their e-prey deliveries significantly; their mates showed a non-significant increase. More unexpectedly, at the nests where females received tail-weights, burdened females showed little reduction in their food deliveries, but their partners substantially increased provisioning anyway. Consequently, the broods received considerably more food than usual. Thus, if the positive male response was to his mate's behavior at all, it could not have been because she was doing less. More generally, we found little evidence that parents are responding to each other's provisioning rate (as required by the Negotiation Model), leading to the conclusion that parental effort is tied more directly to other factors (perhaps brood condition) and is more like a "sealed bid" with independent parental decisions (Schwagmeyer et al. 2002).

We also handicapped male provisioning performance with a second experimental manipulation, this time by surgically inserting small tubes containing time-release testosterone beneath the scapular skin, implanting empty tubes for controls. This produced a more dramatic reduction in male provisioning, as well as a reduction in male

incubation time (62% lower than controls for both measures), but a significant female compensatory increase was observed only during incubation. At that stage of the cycle, testosterone-dosed males appeared to reallocate time and effort to non-parental activities, as they did more singing and behaved more aggressively (both to other males and to their own partners) than control males. These hormone results showed that male and female workloads are strongly inter-related when offspring are still inside eggs, but not after hatching (Schwagmeyer et al. 2005). One interpretation of this difference considers that both parents are likely too busy when seeking and delivering prey items to keep track of each other's contributions (their independent visits to the brood typically last only 1–5 sec and encounter each other only by chance). In contrast, most incubation changeovers are face-to-face and the other changeovers are likely to carry information about when the partner departed (from the lingering tell-tale warmth of the eggs). We are currently exploring the behavioral dynamics of shared incubation in a new series of experiments.

WHEN PARENTING COSTS ARE REDUCED

Parents detecting their offspring are developing ahead of schedule might be expected to reduce their costly provisioning activities, either to use the time and effort for immediate reproductive advantage (especially males that can fertilize additional females) or for maintaining higher personal condition to benefit future offspring. The approach typically used for such load-lightening studies is to make food readily available to the experimental pairs (e.g., a feeder near the nest) and simply assume that a nontrivial amount of the extra nutrients is passed along to the offspring. We took a less trusting route by hand-feeding nestlings with commercial baby bird food twice a day. Specifically, we suspended nutrient powder in warm water to form a thin gruel and squirted it directly down the esophagus of each brood member through a modified syringe. Supplemented broods thus received an extra 25–30% of their estimated Daily Energy Budget, over and above whatever their parents supplied. We sampled parental provisioning as before, averaging ~15 hrs at each of the 23 experimental broods.

Parents did not abridge their food deliveries to these supplemented nests (Mock et al. 2005). Instead, females showed their usual provisioning increase after day 5, but this time their males escalated in lock step, outperforming control males by 25%. This male rate increase did not come at the expense of food quality (e.g., the proportion of e-prey in the diet remained constant). Subsidized nestlings, despite this extra nutrition, neither gained weight more rapidly nor achieved higher mass by banding age, but they recruited into the local breeding population at a somewhat higher rate (11.8%) than matched controls (4.9%).

Thus, it appears males do not automatically divert their attention away from the current brood when parental burdens are lessened, but may respond positively to stronger offspring. Some data on begging call intensities showed that our supplemented broods begged more loudly, suggesting a possible proximate cue underlying paternal responses, but we found no evidence these broods differed visibly from normal (i.e., no mass effects). The asymmetrical responsiveness of the parents to subsidized broods may stem primarily from females already operating near their maximum (a ceiling effect), while males have extra reserves that normally remain unspent, or are channeled elsewhere.

FULL CIRCLE

We close this discussion of our research program where we started with explicit appreciation of our debt to Margaret Morse Nice for demonstrating the value of color bands. The huge amount of time and effort we have invested over the years in building and maintaining study populations of recognizable individual sparrows is a direct reflection on its central role in our work. Of course, numbered metal bands opened many research areas, but the advantage of being able to identify individuals without re-capture and from a distance truly revolutionized behavioral ornithology. Every project described would have been either totally impossible or substantially weaker without that preliminary step. One cannot even be certain that a given subject has not been used already in either the same study (with loss of statistical independence) or in a previous experimental manipulation (with the risk of introducing bias from that earlier treatment) without known individuals. One small celluloid band placed on one special sparrow in 1928 gave so much to so many.

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THE POSTBREEDING MIGRATION OF EARED GREBES

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ABSTRACT.—Eared Grebes (*Podiceps nigricollis*) in autumn make a postbreeding/molt migration from breeding areas in western North America to hypersaline lakes in the Great Basin. We studied their biology in 2001–2006 during this phase of the annual migration near Green River, Wyoming, USA where migrants *en route* to Great Salt Lake, Utah land on industrial ponds. Most evidently originate in the Prairie Pothole Region of North Dakota. The main movement extends from late July to mid-Oetober. Migrants arrive almost daily with the cumulative percentage of transiting birds increasing by about 1% per day. Adult males and females migrate on the same schedule and precede juveniles by 2–3 weeks. Annual differenees in phenology, abundance, age ratio, and wing molt vary with availability of wetland habitats in the main souree area. Data on mass, body eomposition, energetics, and stomach contents indieate a typical flight involves a direct 2–3 day non-feeding migration, whieh is accomplished at night. Grebes are quiescent during the day and do not resume their migration until 45 min after sunset. We documented two undescribed vocalizations, a short-range contact note and one assoeiated with departure. The possibility that Eared Grebe productivity, as inferred from studies of migrants through Wyoming, can provide insight into the status of waterbirds in the source area is worth further investigation. *Received 16 March 2009. Accepted 6 December 2009.*

The autumnal migration of the Eared Grebe (*Podiceps nigricollis*) in North America occurs in two phases. Promptly after the breeding season adults and young undertake a postbreeding migration from nesting areas in the interior to molting/staging sites at hypersaline lakes in the Great Basin (Fig. 1; Storer and Jehl 1985). Nearly the entire North American population stages at Mono Lake, California and Great Salt Lake, Utah from late summer through early winter and then undergoes a poststaging migration to wintering areas in Mexico and southern California (Jehl 1988, Cullen et al. 1999).

Major details of grebe biology during the nonbreeding season are reasonably well established (Cullen et al. 1999; Jehl and McKernan 2002; Jehl et al. 2002, 2003; Ellis and Jehl 2003; Jehl 2007). Most grebes undertake a 800–1,500 km flight, which apparently occurs without feeding, to reach staging lakes (Jehl and Yochem 1986, Boyd et al. 2000). Few can make the trip on a single flight because migration occurs only at night. Migrants passing through western Wyoming toward Great Salt Lake must cross large spans of steppe desert, where rest stops are few and unreliable. Near the town of Green River some encounter an apparent oasis in the form of large (up to 400 ha) and sterile evaporation ponds associated with mining a hydrated form of soda ash (Na_2CO_3) known as trona ($Na_2CO_3/NaHCO_3{\cdot}2H_2O$). Sodium salts in the supersaturated ponds can encrust feathers and lead to mortality. The trona industry has developed a program to reduce potential losses by monitoring the migration, and capturing and rehabilitating afflicted birds through the entire migration season. We took advantage of this exceptional sample to document Eared Grebe biology and behavior during a phase of the annual cycle that had been largely ignored. The data also generated basic information on age ratios, timing and pattern of migration, molt patterns, and annual patterns of production that are essential for understanding grebe biology but which, for logistical and sampling reasons, cannot be obtained at the major fall staging areas (Jehl and Johansson 2002).

METHODS

We studied grebe migration from 2001 through 2006 at the FMC West Vaco and OCI trona ash plants, which are ~15 km apart and 30 km northwest of Green River and 220 km east-northeast of Great Salt Lake (Fig. 1). Each year we visited the sites early in the migration season and instructed staff on Eared Grebe natural history and procedures for collecting data. The staff inspect the ponds several times each day starting about 0700 hrs over the entire fall migration season, from late June through November, and record all species of waterbirds encountered (captured, not captured, found dead). Encrusted birds, predominantly grebes, are captured as quickly as possible, transported to a nearby (1–2 km) treatment facility, washed in warm water to remove external salts, and allowed to rest and dry

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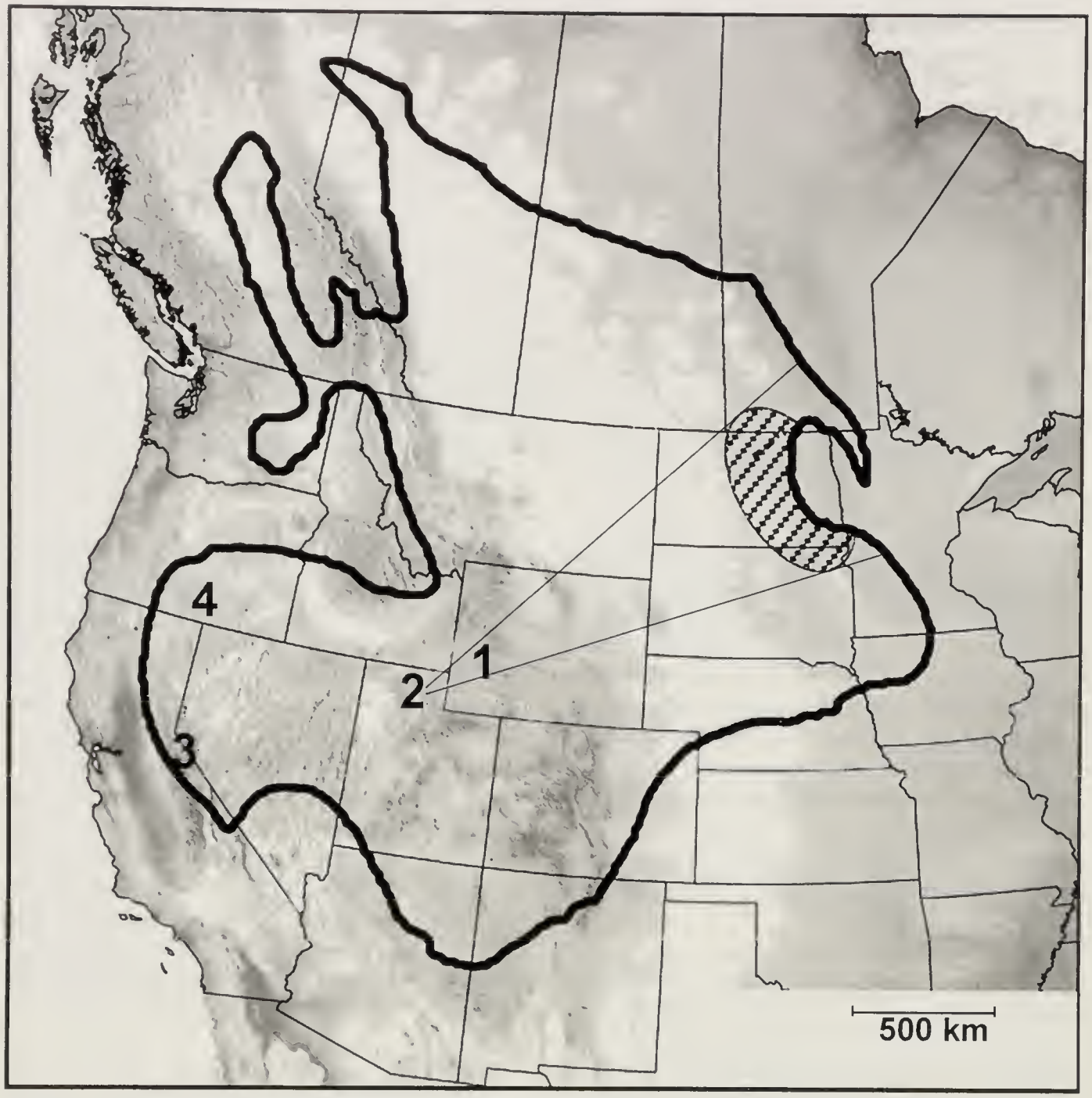

FIG. 1. The major breeding distribution of the Eared Grebe in North America (outlined in black; from Cullen et al. 1999). Great Salt Lake, Utah (2) and Mono Lake, California, (3) hold >1 million staging birds in fall. Most migrants passing through Green River, Wyoming (1) probably originate in eastern North Dakota (cross-hatched). Abert Lake, Oregon (4) is evidently used by some migrants *en route* to the staging lakes. Map by Dan Cole, U.S. National Museum of Natural History.

in a large freshwater tank. In mid-afternoon they are released locally along the Green River (fresh water).

Staff collected data on age, wing molt, and other characteristics as time permitted. Body mass was measured in early afternoon, after the birds had been cleaned of salt deposits and thoroughly dried. Age was recorded as adult (AHY = after hatch year) or juvenile (HY = hatch year) based on iris color: crimson in adults, brown to orange-brown in juveniles. Birds in their second year (SY = hatched in the previous year) have irides that are orange or pale red and would be classified as AHY (Storer and Jehl 1985). Adult males and females were separated by bill length: ≧23.5 mm = male, <23.5 mm = female, a procedure that is >90% reliable (Jehl et al. 1998). We made no consistent effort to sex juveniles because bill growth may not be completed by onset of migration. Grebes were weighed on a digital scale (±1.0 g) after they were cleaned and dried, typically 4–6 hrs after capture (1400 hrs). We

TABLE 1. Eared Grebe migration schedule by age class, 2001–2006, based on birds captured or found dead during autumn migration in southwestern Wyoming.

	Adults			Juveniles			Combined migration	
Year	Migration span	Days	75% complete	Migration span	Days	75% complete	Span	Days
2001	12 Jul–16 Oct	97	1 Sep	14 Aug–6 Nov	85	22 Sep	12 Jul–6 Nov	118
2002	5 Jul–12 Oct	100	7 Aug	10 Aug–16 Oct	68	25 Sep	5 Jul–16 Oct	104
2003	23 Jun–28 Sep	98	3 Sep	19 Aug–24 Oct	67	10 Oct	23 Jun–24 Oct	124
2004	6 Jul–24 Sep	81	19 Aug	20 Aug–1 Nov	84	23 Sep	6 Jul–01 Nov	119
2005	12 Jul–30 Sep	81	6 Sep	10-Aug–11 Nov	94	22 Sep	12 Jul–11 Nov	123
2006[a]							18 Jul–15 Oct	90

[a] No data by age class.

used color of the primaries, brown in unmolted grebes, black in newly-molted, to learn whether wing molt had been completed before grebes left breeding locations.

We observed grebe behavior on the evaporation ponds and in the treatment facility on >40 days (2001–2005), and rehabilitated birds from release through departure on over 30 occasions. We recorded vocalizations in the laboratory and in the field using a Radio Shack Unidirectional microphone (frequency response 0.01–10 kHz), recorded sounds directly to computer hard drive, and analyzed them using ISHMAEL (Mellinger 2001). Body composition and sex identification of birds found freshly dead (<24 hrs) were ascertained by dissection (Jehl 1997). Fat content of migrants was calculated as: fat (g) = 0.76 body mass (g) − 163.54 g (H. I. Ellis and JRJ, unpubl. data).

The source of migrants passing through Green River can only be inferred. Breeding grebes are scarce in eastern Wyoming and across the High Plains. Only a few hundred pairs breed in South Dakota (Drilling 2007), and several thousand in western Minnesota (Boe 1993). Grebes departing Great Salt Lake in early winter fly in a straight line toward wintering areas (JRJ and S. A. Gauthreaux, unpubl. data), and we assume postbreeding migrants behave similarly. Thus, we infer that most Green River migrants originate in the Prairie Pothole Region of North Dakota, where tens of thousands breed (Stewart 1975, Igl et al. 1999). Those originating farther north or south would likely by-pass the trona ponds. The distance from the eastern Dakotas is >1,000 km, requiring a flight of at least 2 days. We examined synoptic weather maps from the northcentral U.S. 2 days prior to 19 large arrivals (36–369 individuals) to investigate if weather influenced the grebes' decision to migrate. We used a paired *t*-test to compare the number of ponds in the northcentral U.S. to the number of grebes encountered near Green River.

RESULTS

Phenology.—Eared Grebes usually arrived between dawn and 1000 hrs. This species avoids flowing water (JRJ and AEH, unpubl. data) and only rarely did grebes land on the nearby Green River, which is only 1 km from some ponds (Julie Lutz and Larry Cherny, pers. comm.). Phenology was similar at both trona plants in all years and the data were combined. The earliest arrivals appeared in late June (Table 1). Small numbers (1–15) arrived almost daily (Fig. 2A) during the main influx, 1 August–2 October; the cumulative increase averaged 1.3% per day (Fig. 2B). Arrivals slowed to 0.5% per day from 3 to 15 October before ceasing in early November. Yearly patterns were similar despite an occasional pulse of >100 birds or variation in the total encounters, and paralleled those documented in 1992–1995 (Jehl and Johansson 2002).

Age and Sex Ratios.—Adults migrated earlier than juveniles (Fig. 3), 75% by the first days of September (Table 1). Those arriving before 1 August were probably nonbreeders or failed breeders. Juveniles began to appear in mid-August and, in most years, 75% passed through by 25 September. The sex ratio of adults (2001, 2002, 2005; n = 396 males, 380 females) did not differ from 1:1 overall or in any individual year. More juveniles were classified as females than males (2001, 28:15; 2002, 67:58; no data for other years), probably because growth had not finished, inflating the apparent proportion of the smaller females.

Wing Molt.—Data on wing molt were obtained in 2001 and 2002. The pattern was similar in both

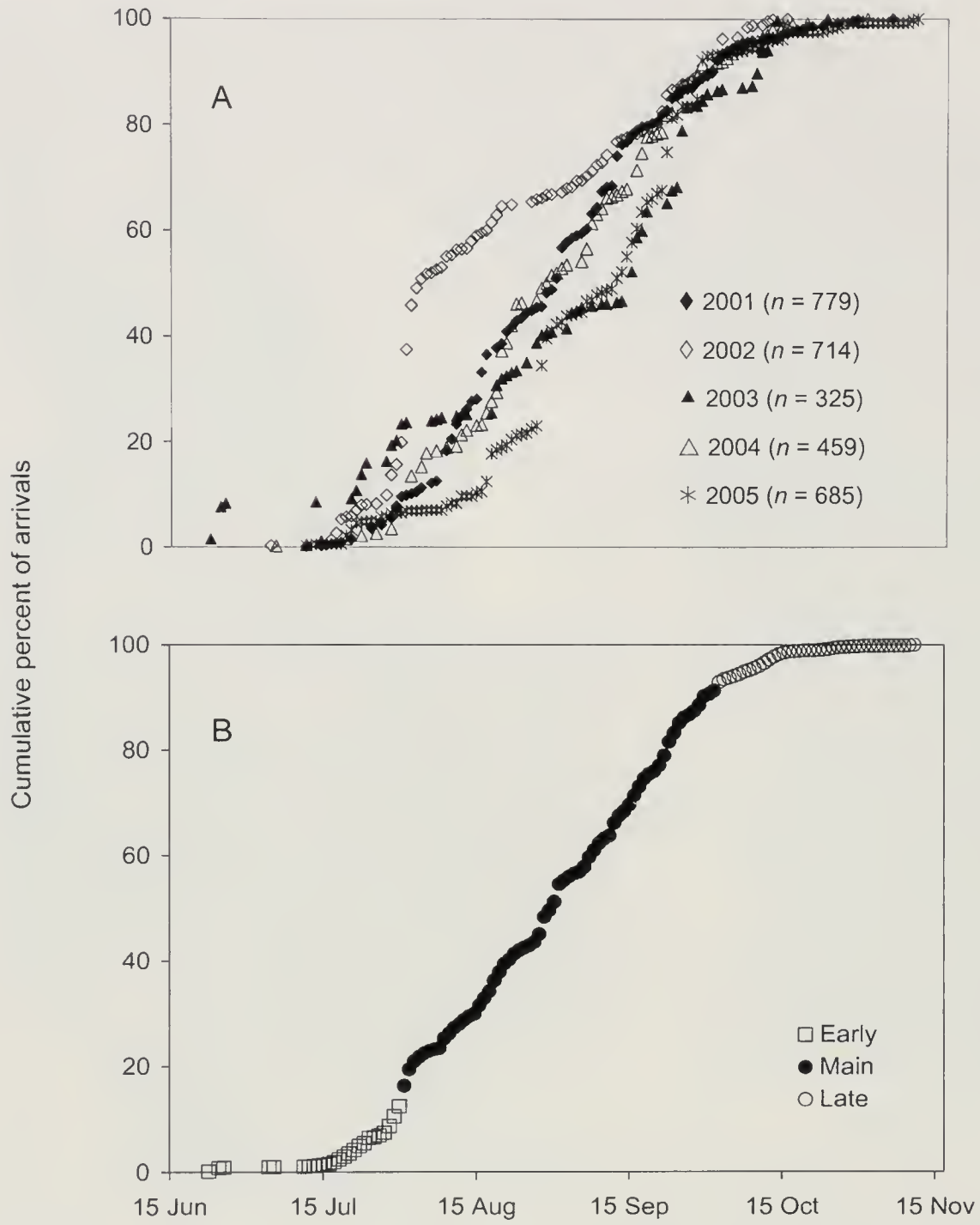

FIG. 2. Phenology of Eared Grebe autumn migration in southwestern Wyoming, 2001–2005. A. Individual years; 2001–2005, *n* = total grebes recorded at FMC and OCI plants. B. All years combined.

years. The first migrants with new remiges arrived in mid-August and the frequency increased as the season progressed (Fig. 4); by 20 September all passage adults had molted. The frequency of molt in breeding areas was greater in 2001 (21% of 206 adults) than in 2002 (7% of 425).

Body Mass, Body Composition, and Stomach Contents.—Mass did not vary from year to year. The mean (± SD) was 297 ± 32 g for adults with males averaging 7.5% heavier than females, and 295 ± 35 g for juveniles (Table 2). There was no consistent or significant pattern by males and females, age, or date in the 3 years for which we have adequate data. Carcasses showed the enlarged flight muscles and reduced digestive organs characteristic of birds that had reconfigured body composition prior to migrating. Body and component masses were greatly reduced in comparison to migrants elsewhere known to have been in migration for only one night (Table 3). Gizzards lacked a pyloric plug and were nearly devoid of digestible food; the weight of non-feather debris averaged about 0.4–0.5 g, most of which was finely ground and unidentifiable. Eight of 10 gizzards examined in detail in 2006 contained unidentified insect material—mostly

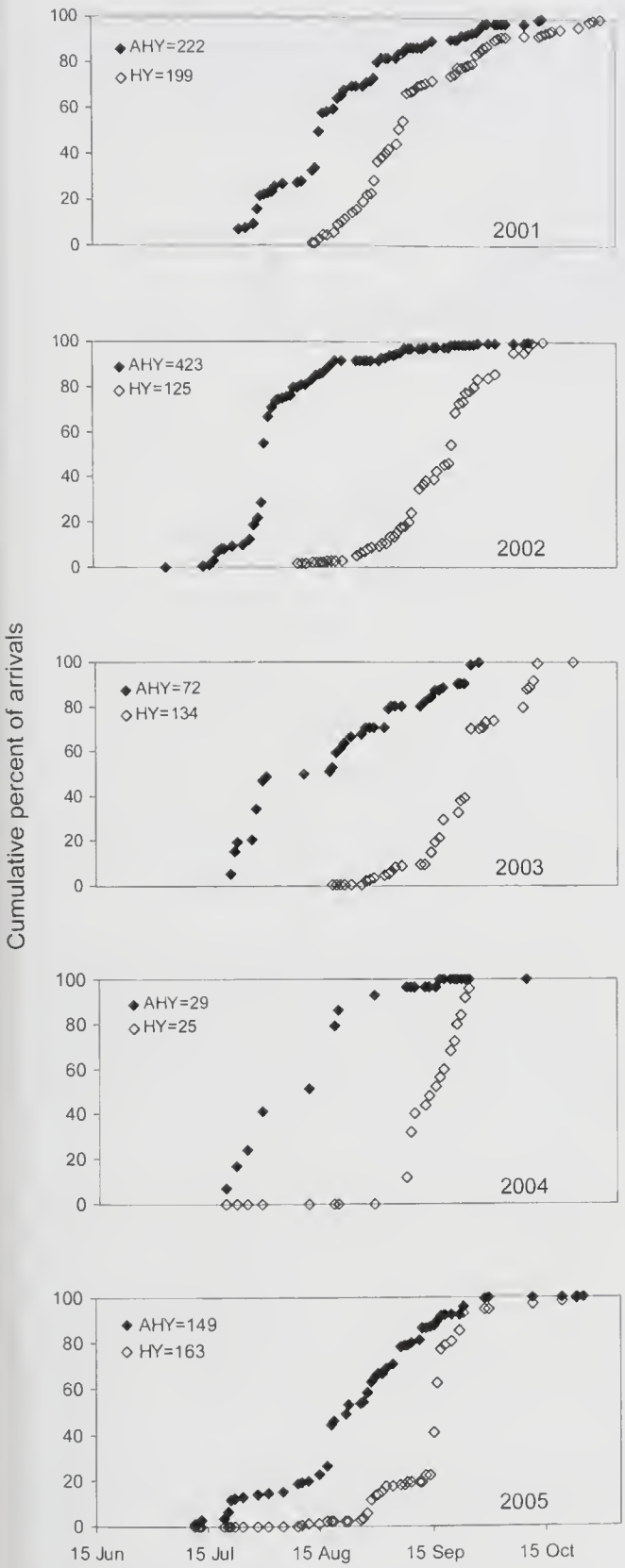

FIG. 3. Arrival schedule of adult (AHY) and juvenile (HY) Eared Grebes in southwestern Wyoming, 2001–2005.

fragments of exoskeleton from surface-dwelling aquatic beetles and alkali flies (*Ephydra* spp.); two contained brine shrimp (*Artemia* spp.) eggs, four–miscellaneous seeds, three—fragmentary plant material, three—jaws of nereid worms (n = 3, 6, and 200–300), and two—small bits of grit or sand. Eight also contained feathers, which were extremely worn in five cases, but freshly ingested (1–2 days) in three others.

Behavior During the Day.—Grebes that landed on the trona ponds remained largely inactive throughout the day, as is characteristic of birds stopping over in natural situations. They did not attempt to drink or feed, nor did they dive, unless pursued for capture. Typical of grebes, they preened continually. If salt crystals began to form, they increased preening efforts, pulling several feathers through the bill and using vigorous head-shaking to flick off adhering crystals. As encrustation increased they moved closer to shore, often attempting to haul out. Unimpaired birds remained on the ponds and evidently departed successfully after dark.

There was little variation in behavior of rehabilitated birds upon release. They swam directly to the middle of the Green River and engaged in comfort movements (bathing, stretching, preening, adjusting plumage, drinking) for up to a half-hour; some also made shallow and brief (8–15 sec) dives, evidently to readjust plumage. Subsequently they began to investigate their surroundings, swimming up- or downstream until they encountered rapids or other barriers and then reversed course. They then moved into secluded sites near shore, out of any current, and rested or slept until evening.

Departure.—Sunset is a key time. Grebes began to become active a few minutes after the sun dipped below the horizon, when they returned to mid-river, and began predeparture activities. These included ritualized preening of the back and scapulars, one or two short practice flights (always upstream), and group diving, submerging, and surfacing in near-unison. As dusk deepened the birds became quiescent for several minutes. Then, 40–45 min after sunset, when it was almost completely dark, they performed a few intention movements, consisting of pumping the head up and down and giving soft calls. Then, with no further signals, they flew upstream ~1 m above the river for about 100 m or so before climbing and disappearing westward. Small groups left as a unit but, when relatively large numbers (>15) were present, flights could be spread over 3–10 min. Any that did not leave swam back to shallow water and rested without feeding until the next sunset.

We noted *zugunruhe* in captive grebes twice. Six adults captured before noon on 17 August

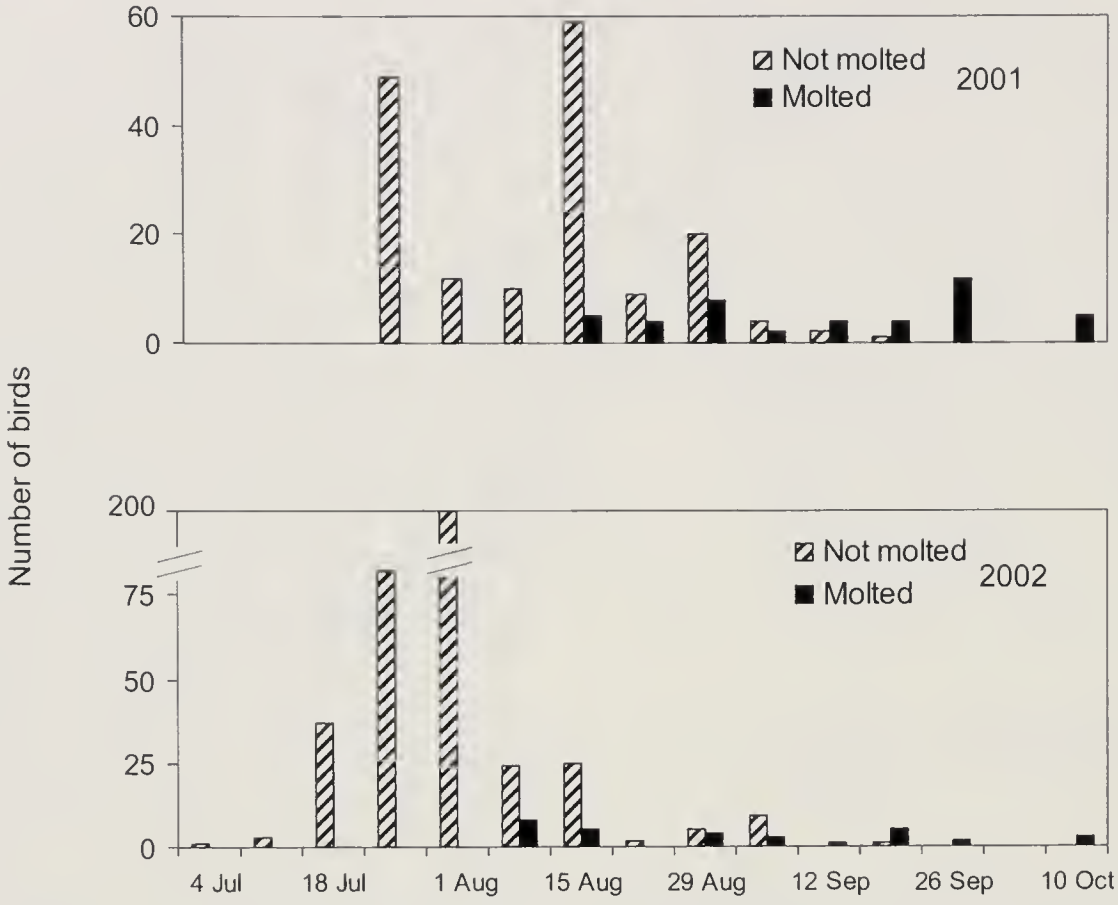

FIG. 4. Timing of remige molt of Eared Grebes migrating though southwestern Wyoming, 2001 and 2002. Data presented in weekly intervals.

2001 were retained overnight for metabolic studies. They became agitated at 2100 hrs (46 min after sunset), despite having had no view of the sky or access to natural light for 9 hrs, started to vocalize, and swim actively for about 30 min (H. I. Ellis, pers. comm.). Other birds released earlier that day departed between 2054 and 2112 hrs. In another case, birds in a dark box being transported to a release site in the early evening suddenly became restless and started calling 27 min before sunset. This behavior was not observed when birds were released earlier in the day (Julie Lutz, pers. comm.).

Vocalizations.—Two vocalizations were recorded (Fig. 5). Both were compound sounds, made up of more than one unit and within the frequency range (1–5 kHz) of calls associated with breeding, but their structures were distinct. The "A" call consisted of three frequency-modulated downswept vocalizations in a 1.2 to 1.5 kHz bandwidth. We heard it as grebes were preparing to depart and immediately before the actual takeoff. The "B" call, reminiscent of a soft amphibian-like grunt, consisted of a patterned series of 5–11 individual pulses with a consistent interpulse interval of 0.025 sec. Each series was repeated

TABLE 2. Mass (g), by males and females, and age of migrating Eared Grebes captured in autumn migration, southwestern Wyoming, 2001–2005.

	Adult males		Adult females		All adults		Juveniles	
Year	*n*	Range ($\bar{x}$ ± SD)	*n*	Range ($\bar{x}$ ± SD)	*n*	Range ($\bar{x}$ ± SD)	*n*	Range ($\bar{x}$ ± SD)
2001	83	249–409 (305 ± 29)	75	210–345 (277 ± 23)	158	210–409 (292 ± 30)	191	197–388 (299 ± 35)
2002	223	223–389 (305 ± 30)	210	200–394 (285 ± 30)	424	200–394 (296 ± 31)	125	222–372 (287 ± 31)
2003[a]					10	228–332 (288 ± 31)	31	218–360 (291 ± 35)
2004[a]					29	225–367 (304 ± 33)	25	197–348 (290 ± 35)
2005	68	270–396 (316 ± 28)	79	217–390 (297 ± 32)	147	217–396 (306 ± 32)	162	213–398 (297 ± 36)
All years	374	223–409 (307 ± 30)	364	200–394 (286 ± 30)	768	200–409 (297 ± 32)	534	197–398 (295 ± 35)

[a] No data by categories of males and females.

TABLE 3. Body composition (g) of Eared Grebes found freshly dead at the end of a migration: Green River, Wyoming, August–September 2001–2006, and Iron Mountain, California, January 1993 (from Jehl 1997: Table 1).

Description	Green River, Wyoming		Iron Mountain, California	
	n	Range ($\bar{x}$ ± SD)	*n*	Range ($\bar{x}$ ± SD)
Mass	25	240–330 (280.2 ± 24.0)	7	312–423 (368 ± 41.4)
Breast	24	16.0–23.2 (19.7 ± 1.9)	7	21.7–27.0 (24.0 ± 1.9)
Heart	26	2.7–4.7 (3.6 ± 0.4)	7	4.5–5.4 (5.0 ± 0.3)
Intestine	10	7.5–13.6 (9.7 ± 1.7)	7	7.0–12.4 (10.2 ± 1.9)
Leg	10	11.1–14.4 (13.1 ± 1.2)	7	14.7–20-1 (17.1 ± 2.0)
Liver	26	6.1–11.8 (8.8 ± 1.2)	7	7.8–13.7 (10.6 ± 1.9)
Stomach	26	6.6–15.5 (10.6 ± 2.1)	7	9.4–13.3 (11.2 ± 1.3)
Stomach contents	26	0.1–5.6 (1.2 ± 1.2)	7	1.6–7.0 (2.7 ± 1.8)
Estimated time in flight		36–60 hrs		9.3 hrs
Fat stores		20.6–86.4 (49.7 ± 17.7)		72.6–151.4 (112.9 ± 30.6)

five times within a eall. The interval between the first and seeond series was 3.0 see, while the interval between the 2nd, 3rd, 4th, and 5th series was 2.0 see. The fundamental peak frequeney approximated 1.5 kHz with harmonics. More than 50 ealls were reeorded in 10 min from a tank holding 28 individuals.

Weather and Migration.—The main souree of migrants at Green River is probably the Prairie Pothole Region of North Dakota. Synoptie weather maps showed calm eonditions prevailed there at dusk 2 days prior to all major arrivals at Green River. In all eases, winds were <5 km/hr, generally from the NE-SE; in 15 eases a eold front had passed 1–2 days earlier.

DISCUSSION

Eared Grebes migrating through Wyoming *en route* to fall staging areas exhibited behaviors that had not been documented elsewhere, ineluding energy-saving sluggishness by day, *zugunruhe*, striet correspondence of departure with onset of near-total darkness, and unique voealizations.

Our finding that adults migrated earlier than juveniles had been established in breeding areas and at Mono Lake (Jehl 1988, Cullen et al. 1999), but the pattern laeked detailed quantification. That adult males and females migrate on the same sehedule was not unexpected, because adults split the brood, eaeh providing a similar level of eare for about 2 weeks, and then leave before the young can fly (Cullen 1998). Some adults were known to eomplete wing molt in breeding areas (Storer and Jehl 1985, Jehl 1988). The Wyoming data, supplemented by >5,000 individuals banded at Mono Lake over two deeades (JRJ, unpubl. data), indieate that about 11% of adults molt before migrating, and that frequeney of molt inereases as the season progresses and is greater in years when grebes remain longer in breeding areas.

Eared Grebes are generally silent during migration. The two undeseribed ealls we reeorded were within the frequency range (1–5 kHz) of calls associated with breeding, but their struetures were distinet (spectrograms in Cullen et al. 1999). We consider the "B" call a short-range eontact note. The "A" eall was assoeiated with departure. Eared Grebes migrate in the dark, depart staging areas in floeks, and are susceptible to mid-air collisions (Jehl 1998). Whether voealizations or other sounds are used to minimize that risk remains to be investigated.

From Breeding Areas to Staging Lakes: Evidence for a Direct, Non-feeding Flight.—Eared Grebes reorganize their body eomposition before departing staging and breeding areas (Jehl 1997). Departure mass approximates 400–450 g, whieh deereases to 350–370 g after an overnight flight (Jehl 1993, 1994, 1997, 1998). Wyoming migrants averaged ~300 g, >50 g lighter, indicating they had been *en route* for at least 2 days. Their stomaehs and intestines were small and essentially empty, confirming a nonfeeding migration and indieating they had ceased feeding and eleared their gut several days before departing (Jehl 1997). Meteorologieal data support earlier findings (Jehl and Johansson 2002) that grebes depart breeding areas in periods of calm weather. There is no time for a leisurely migration, as southbound adults begin to pass through Green River as early as late July–the same time that departures are noted in breeding areas and migrants appear at the major staging lakes (Jehl 1988, Cullen et al.

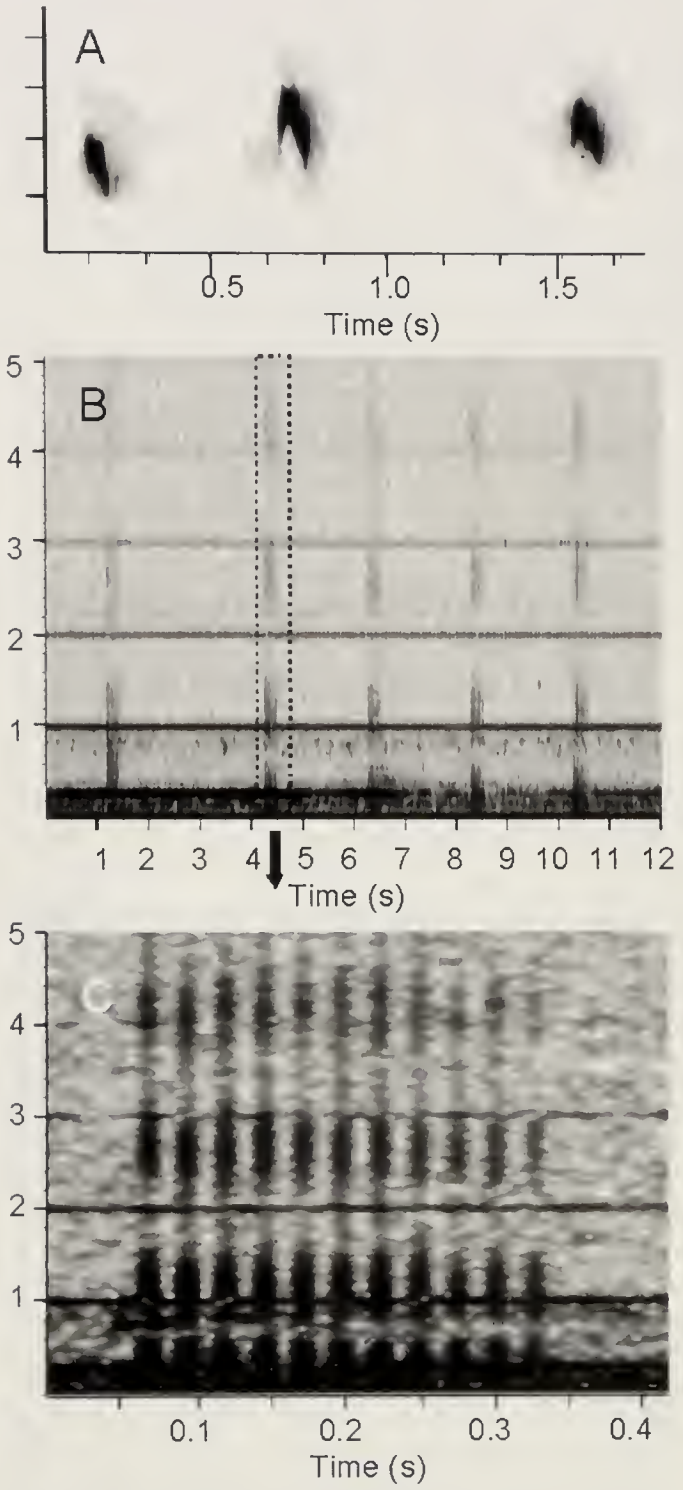

FIG. 5. Vocalizations of migrating Eared Grebes, Green River, Wyoming, 15 September 2005. A. Type "A" call (sample rate 20 kHz, 512 FFT). B. Type "B" call (sample rate 20 kHz, 512 FFT) showing the entire call, which consists of five series of pulses. C. Fig. 5B expanded to show individual pulses.

1999). They do not feed during this movement, and migrants leave stopover locations the evening after they arrive. Thus, weather conditions appear to have little effect once the decision to migrate has been made.

Energetics.—Migrating across arid lands is a challenge (Jehl 1993, 1994; Cullen et al. 1999; Jehl et al. 1999, 2003). Grebes leaving Green River after rehabilitation averaged about 293 g and would be expected to reach Great Salt Lake weighing 271 g with 41 g of fat remaining (H. I. Ellis and JRJ, unpubl. data). This estimate is based on flight costs of 6 g fat/hr (vs. 7.1 g/hr for 400–450 g migrants; Jehl 1994) and a flight time of 3.7 hrs at 60 km/hr (Cullen et al. 1999). The minimal weight for healthy adults is ~240 g (Jehl 1988, Anderson et al. 2007; JRJ, unpubl. data), and migrants need to depart Green River at ≥262 g, which includes 85% of our sample (Fig. 6). Laying over 1 day would require catabolizing at least an additional 17 g of fat (0.7 g/hr resting rate × 24 hrs; JRJ and AEH, unpubl. data). Those delayed for 2 days would deplete nearly all remaining fat and require an additional stop to rebuild the digestive organs and refuel before continuing (Hume and Biebach 1996). The rate of weight gain in staging grebes is 3–4 g/day (Jehl 1988). Consequently, migrants originating more than a 3-night flight from the staging areas (~1,500–1,600 km) probably require a stopover of several weeks or more to accumulate sufficient fat stores to continue. The only present candidate locality for a regular stopover is saline Lake Abert, Oregon where 5,000–7,000 migrants have been reported in September and early October (Jehl 1988).

Annual Differences.—Timing and pattern of migration differed from year to year. Adults and young in 2001 passed through steadily in their respective periods; 75% of adults migrated by 1 September, 21% of adults underwent wing molt before migrating, and juveniles comprised 47% of the migrants. In 2002, 75% of adults migrated 3 weeks earlier, only 7% had molted, and juveniles were few (23%) and concentrated in the last half of September. We consider 2001 a year of successful breeding, whereas in 2002 most adults left too early to have bred successfully, and the relatively few young evidently resulted from late nesting. These differences are probably indicative of habitat loss resulting from the eastward shift into the Dakotas of the severe drought that had beset the western U.S. since the late 1990s (U.S. Drought Monitor maps for 29 May 2001 and 28 May 2002, www.drought.unl.edu/dm/archive.html). Our view that North Dakota is a main source of Green River migrants is supported by the significant relationship (t = 4.33, $P < 0.001$) between the number of grebes encountered near Green River in autumn and the

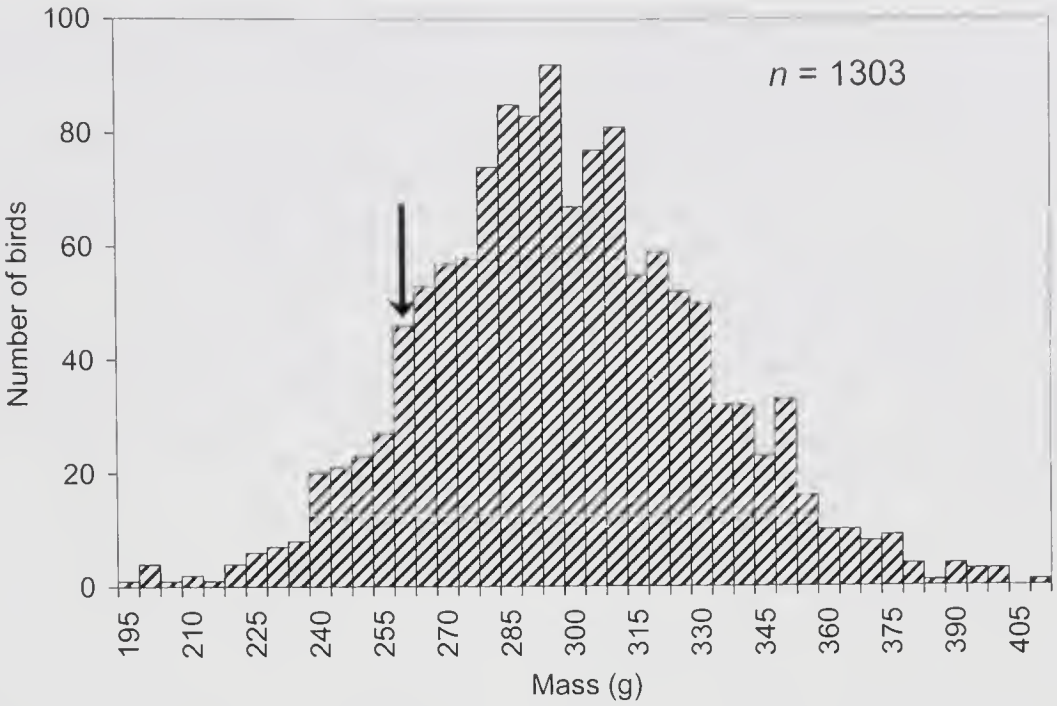

FIG. 6. Mass of Eared Grebes (adults and juveniles combined) captured at Green River, Wyoming, 2001–2005. Arrow indicates estimated minimum mass needed to reach Great Salt Lake without laying over or making an additional stop.

number of May ponds in the northcentral U.S. by year (Fig. 7).

Patterns from other years are less clear. There was an early exodus of adults in 2003, yet nearly half remained in breeding areas into September; juveniles migrated much later than in other years, but comprised a high percentage (65%) of the population. Evidently conditions were poor early, but breeders able to take advantage of late-summer rains fared well, a pattern also inferred from studies of waterfowl (USDI 2003). Data in 2004 were too few for analysis. There was a steady passage of adults in 2005 when juveniles were plentiful (52%), but concentrated late in the season.

Are the Data Representative?—One might question whether a sample from industrial ponds fairly represented the population passing through

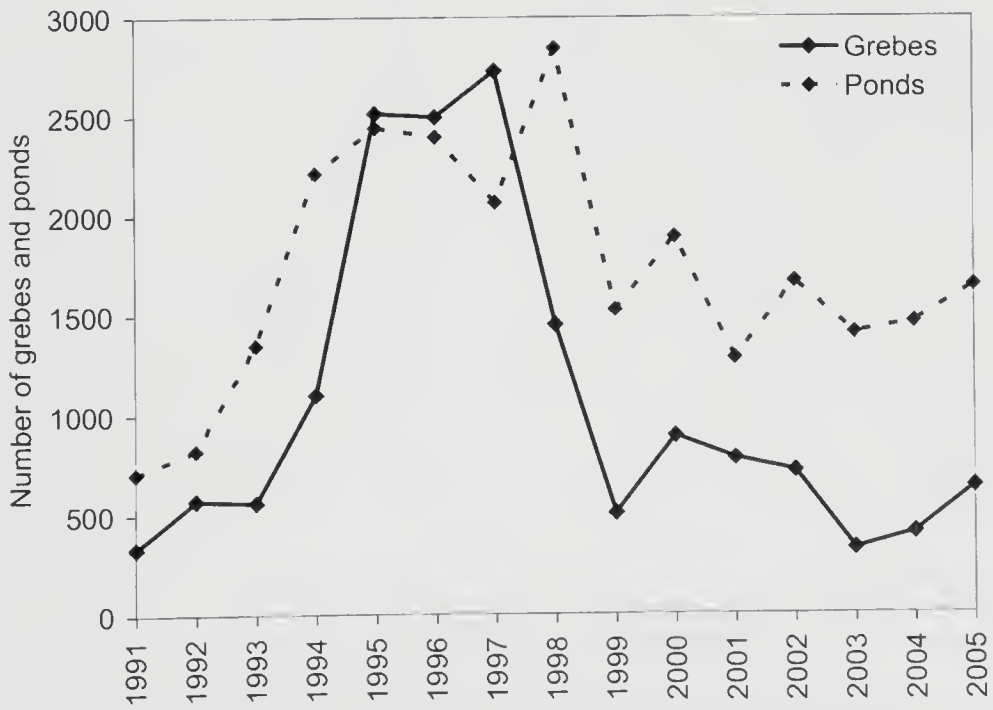

FIG. 7. Number of Eared Grebes encountered at trona evaporation ponds in autumn in southwestern Wyoming and number of spring ponds (in thousands) in the northcentral U.S., 1991–2005. Pond data from USDI (2005).

the region or, perhaps, was biased in favor of inexperienced or unfit birds that had dropped out before they could reach Great Salt Lake. In the latter case, one would expect juveniles to predominate and average lighter than adults. However, adults were as numerous as juveniles, body masses of the two groups were identical, and most birds had sufficient reserves to reach staging areas. In addition, our data on migration timing and intensity parallel those gathered at another series of industrial ponds near Kemmerer, Wyoming, 100 km west-northwest of Green River (Jehl and Johansson 2002). We conclude the Green River sample was derived from healthy birds on a normal migration that interrupted their flight to seek shelter at dawn. Our sample was not biased by variation in timing of the breeding season, because it was compiled over the entire migration period. Thus, our encounter rates and age ratios reflect survivorship to migration in the source area. The wetland habitats occupied by Eared Grebes are also used by waterbirds whose breeding success is difficult to assess (Johnson et al. 2009). The possibility that data from migrating grebes might provide an independent index to annual variations in production of other marsh and water birds in the source area warrants investigation.

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POSTFLEDGING AND NATAL DISPERSAL OF CRESTED IBIS IN THE QINLING MOUNTAINS, CHINA

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ABSTRACT.—Natal dispersal is common among many bird species with females usually dispersing farther than males. We examined postfledging and natal dispersal ecology of Crested Ibis (*Nipponia nippon*) in the Qinling Mountains, China by marking nestlings with either color bands or radio transmitters. Family groups, consisting of juveniles after fledging and their parents, dispersed progressively farther from nest sites after fledging in a southerly direction with a mean (± SD) direction of 189.2 ± 46.5° and a mean distance of 20.3 ± 7.0 km. Mean natal dispersal distance of females (9.6 km) was significantly greater than for males (5.9 km) ($t = 2.14$, $P = 0.03$). Most individuals moved southeasterly from natal areas and dispersal movements of individual ibis were concentrated at the mean direction ($\mu = 185.6°$, $s = 86.1°$). First reproduction by females (3.64 ± 1.36 years) was not significantly earlier than for males (4.17 ± 1.47 years). The results of this study will be useful for reintroduction programs for critically endangered species. *Received 20 January 2009. Accepted 20 November 2009.*

Dispersal, a common response of many birds to habitat diversity, is of substantial interest to animal ecologists due to its importance in population ecology and management (Clobert et al. 2001). Despite its importance, the study of animal dispersal was primarily descriptive until the 1990s (Kendall and Nichols 2004). Walters (2000) suggested that ornithologists should focus on studying dispersal and dispersal biology of birds is gradually becoming better understood (Powell and Frasch 2000, Hansson et al. 2002, Paradis et al. 2002). Recent studies have used mark-recapture techniques (Paradis et al. 1998), intensive observations of marked individuals (Koenig et al. 2000, Pyle 2001), and radiotelemetry (Walls and Kenward 1998, Lang et al. 2002). Indirect techniques, including genetic markers (Horn et al. 1996, Wang and Trost 2001) and stable isotope analysis (Hobson et al. 2001), have also been used.

The Crested Ibis (*Nipponia nippon*) was once one of eastern Asia's most widespread and familiar birds. However, deforestation and destruction of their habitat led to successive extinction of Russian, Korean, and Japanese populations in the 20th century (Yamashina 1967, Archibald et al. 1980). The Chinese Crested Ibis population, once also thought to be extinct since the 1960s, was rediscovered in Yangxian County in Shaanxi Province at the end of a 3-year (1978–1981) survey by a research group from the Chinese Academy. The survey covered nine provinces including Liaoning, Gansu, Hebei, Shandong, Henan, Anhui, Jiangsu, Zhejiang, and Shaanxi (Liu 1981). The single remnant population in Yangxian, comprised of only two pairs and three chicks survived in the remote Qinling Mountains at an altitude of 1,200 m where human exploitation was relatively limited (Shi et al. 1989, Shi and Cao 2001). The wild population has increased from seven to ~600 individuals following protection and management of this area, and its range has expanded to ~3,000 km^2 to lower elevations in the past 29 years.

The Crested Ibis population has been intensively studied for nearly three decades including breeding habits (Shi et al. 1989), gender identification (Li et al. 2001), habitat use (Liu et al. 2003), genetic diversity (Zhang et al. 2004, He et al. 2006), and reproductive success (Yu et al. 2006). However, postfledging and natal dispersal of this population remains unclear. We studied the dispersal ecology of Crested Ibis using colored plastic and numbered bands, combined with radiotelemetry, during 1987–2002.

METHODS

Study Area.—We conducted fieldwork for 16 years (1987–2002) in Yangxian County in the Qinling Mountains of southern Shaanxi

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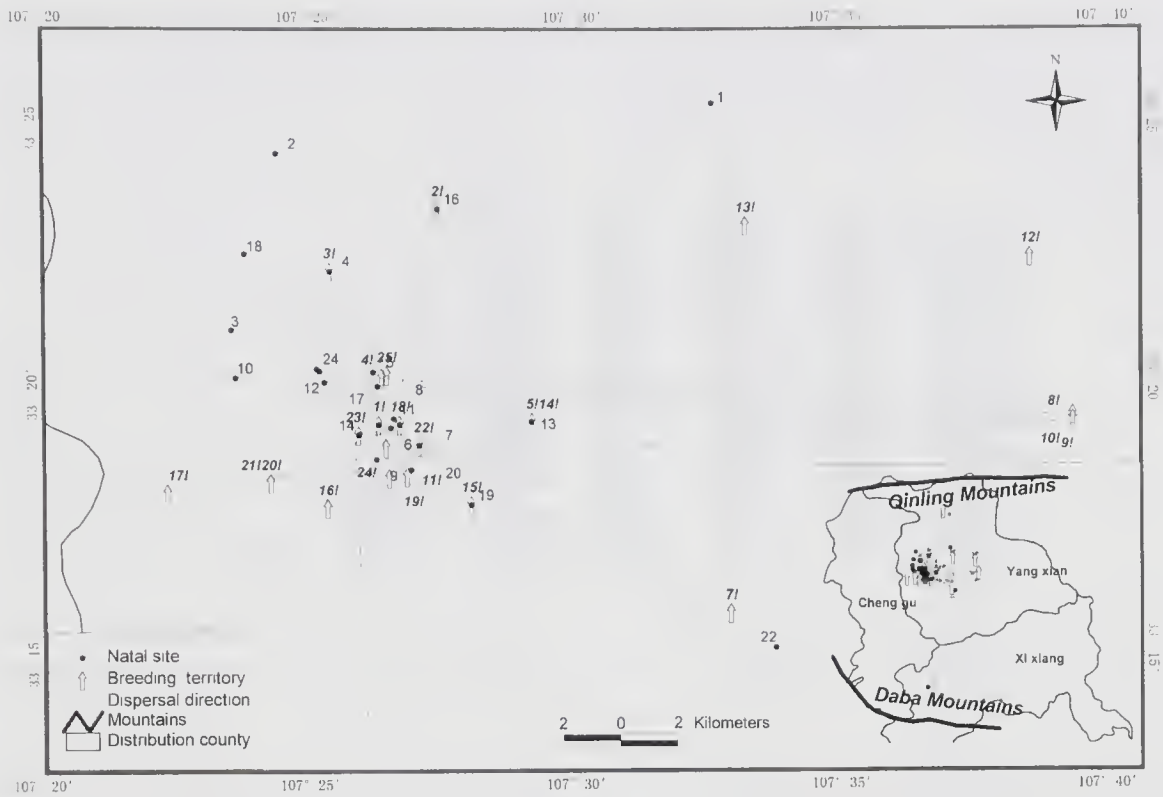

FIG. 1. Dispersal of Crested Ibis (n = 25) from natal site to breeding territory. The insert at the lower right shows the relative position of the study area.

Province, China (33° 02′–33° 43′ N, 107° 11′–108° 03′ E; Fig. 1). This area is used by Crested Ibis for breeding territories for adults and rearing sites for young. More than 80% of the areas used are primarily deciduous broad-leaf forests where the dominant tree species include cork oak (*Quercus variabilis*), Chinese pine (*Pinus tabulaefornis*), Chinese red pine (*P. massoniana*), and oriental arborvitae (*Platycladus orientalis*). One nesting area is in even-aged cork oak forest characterized by trees with diameter at breast height (dbh) ranging from 42 to 80 cm, and canopy heights ranging from 17.2 to 32.6 m, planted in a graveyard of the Qing Dynasty in the 1800s (Shi and Cao 2001). Areas to which both adults and young dispersed during August–October are characterized by hills with many artificial ponds and reservoirs, and vast farmlands along the Hanjiang River. Area studied was expanded each season to include sites where both young and adults dispersed.

The average annual air temperature was 12–14° C reaching a minimum in January (−10.1° C) and a maximum in July (38.7° C) with a frost-free period of 238 days. Average monthly rainfall ranged from 4 mm in January to 161 mm in July with most occurring between July and September (Youngxian County meteorological station).

Banding and Radiotelemetry.—Crested Ibis prefer to live near human settlements (Li et al. 2002) making it possible to find all nests and mark all nestlings (304 individuals) (Table 1). We banded nestlings with a combination of colored plastic and numbered bands at 24–26 days of age when their tarsi were fully developed but before they were able to leave the nest. We checked and verified the band color combination and number of both juveniles and adults at roost sites in wintering areas, and at nests in breeding territories each year. We also recorded the location, altitude of nesting and roosting site, as well as age, gender, behavior, and color markings of all individuals present. We made repeated observations to confirm identity when a banded adult was encountered on a breeding territory. We placed 15-g radio transmitters on Crested Ibis nestlings weighing 1,350–1,450 g between days 23 and 25 in the 35-day nestling period. Radio transmitters, which could transmit for 6 months, were attached dorsally with the antenna pointing toward the tail using a harness of nylon elastic string tied under each wing, leaving room for growth of the wings and pectoral muscles. Three nestlings from different broods were radio-marked in 1990, 1992, and 1994, respectively. Family groups consisting of siblings and their parents formed

TABLE 1. Observation rates of banded nestlings and natal sites of Crested Ibis. Values in parentheses are the number of reobservations of banded vs. all nestlings banded. Sequence number of natal sites (1–25) is consistent with Figure 1.

Year	Observation rate %	Natal sites
1987	33 (1/3)	1
1988	43 (3/7)	2,3
1989	57 (4/7)	1,3,16
1990	50 (3/6)	2,3,4
1991	50 (2/4)	11,16
1992	43 (3/7)	5,7
1993	0 (0/2)	
1994	17 (2/12)	17,18
1995	0 (0/10)	
1996	7 (1/14)	14
1997	32 (7/22)	5,15,17,19,22
1998	50 (8/16)	5,9,15,16,25
1999	31 (31/39)	6,13,23,25
2000	15 (5/33)	11,14,16,18
2001	12 (22/55)	5,14,17,18,20,21
2002	15 (15/67)	7,12,19,24
Totals	24 (73/304)	25

wandering flocks for nearly 3 months. We were able to locate radio-marked individuals, as well as other birds with colored and numbered bands in the same flock, using programmable receivers (TRX-1000S, Wildlife Materials Inc., Carbondale, IL, USA) and 3-element, hand-held antennas.

Bird Visits and Surveys.—We considered marked Crested Ibises as new breeders when they first performed territorial displays (vocalizing, perching near, or flying close to the observers) while eggs or chicks were present in the nest from early January to mid-February. The frequent and hoarse calls of the pair, especially the male, were used to locate breeding birds. We classified males and females of each pair by observing copulation behaviors during courtship. Age of each bird was based on individual identification, using a 40× telescope, of the colored plastic or numbered bands on their legs.

We defined natal dispersal as movement from hatch site to first breeding or potential breeding site (Greenwood and Harvey 1982), and post-fledging dispersal as movements of young after they became independent of their parents and left the natal territory to move to wintering areas (Bull et al. 1988). Crested Ibis usually start to breed when they are 3-years of age (occasionally 2 or 4–7 years) (Zhai and Wang 1994, Lu et al. 1997). Relocated individuals were grouped into two data sets: yearlings and ≥2 year-old individuals. These data sets were analyzed separately for differences in distance moved by yearlings and those dispersing from natal areas until they became established on breeding areas. The distance moved by male and female yearlings was combined as individuals could not be identified prior to performing courtship displays.

We recorded the location of birds re-encountered using Global Positioning System (GPS) receivers. The distance moved was calculated on 1:50,000 topographic maps as a straight-line between natal sites and first breeding territories for natal dispersers or post-fledging areas for juveniles. We estimated the azimuth from the nest location to the final known location for each dispersing ibis (final direction). We calculated the mean final direction (μ) and the angular deviation ($\check{s}$) around the mean final direction for each cohort, and used Rayleigh's z to test for directional pattern within cohorts (Zar 1996). All circular analyses were conducted using Oriana for Windows (Version 2.0) (Oriana 2003).

Non-parametric statistical treatments (SPSS for WINDOWS, Version 11.5) were used for tests if dispersal data was not normally distributed. We report means ± SD unless otherwise noted, and statistical tests were considered significant at $P = 0.05$.

RESULTS

Postfledging Dispersal of Young.—We followed 36 yearlings of the 304 nestlings banded including three radio-marked individuals from fledging through dispersal to areas used for breeding. All natal home ranges were close to paddy fields near human settlements at the edge of even-aged, mature oak-pine forests characterized by 25–80 cm dbh, and canopy heights ranging from 15 to 33 m. Stands ranged in age from 25 to 183 years.

One movement pattern was used by Crested Ibis family groups during postfledging dispersal in all cases. Movements of family groups prior to dispersal were centered on nest sites, and areas within the nest territory were visited repeatedly up to time of dispersal. The distance between family groups and their natal nest sites was 0.54 ± 0.67 km. Nest territories were occupied for an average of 21.1 ± 10.2 days ($n = 36$) from time of fledging (38–40 days of age) to dispersal. Family groups, composed of chicks and adults, moved progressively farther (Fig. 2) along the

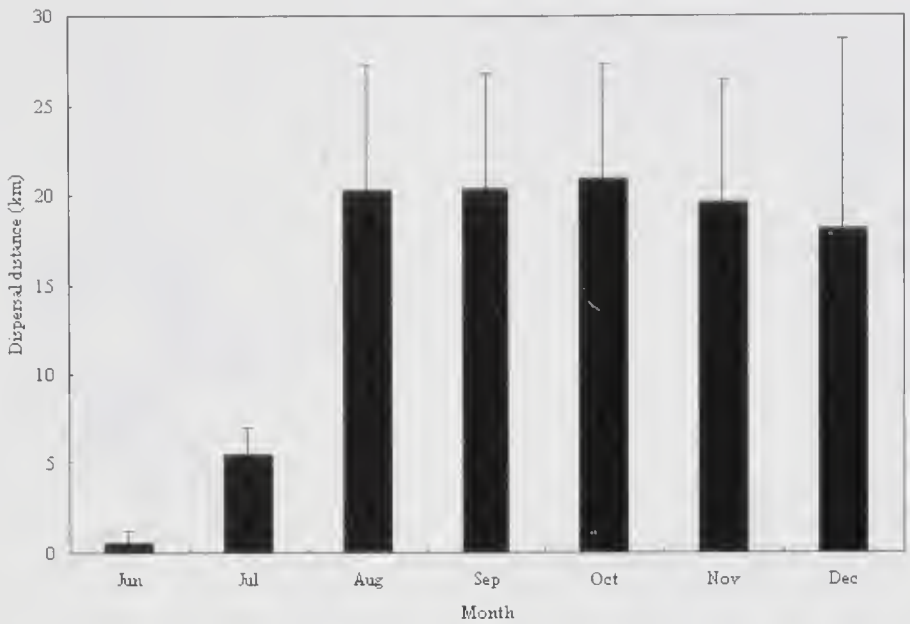

FIG. 2. Distances ($\bar{x} \pm$ SD) of post-fledging movements of young (June–December, $n = 36$).

tributaries of Hanjiang River in a southerly direction with a mean direction of 189.2 ± 46.5° ($n = 36$ ibis). Siblings of each brood increasingly become independent of their parents at the beginning of August and all young, as well as adults from different families, formed wandering flocks in post-dispersal areas characterized by a sweep of distant hills with many artificial ponds, reservoirs, and vast farmlands along the Hanjiang River. Mean dispersal distance was 20.3 ± 7.0 km ($n = 36$). Young took 51.4 ± 8.1 days (range = 40–64 days) to disperse from their natal area to their post-dispersal range, where most remained for nearly 2–3 years until they became sexually mature. Most immature individuals (2–4 years of age) spent summers in wintering areas 15.5 ± 4.3 km ($n = 25$) south (191.5 ± 33.6°, $n = 36$ ibis) of their first breeding sites. The average elevation of the roosting sites (560.0 ± 55.6 m, $n = 15$) in wintering areas was significantly lower than that in first breeding sites (786.5 ± 56.8 m, $n = 25$) ($t = 12.3$, $P = 0.000$).

Natal Dispersal Distance.—Seventy-three (36 males and 37 females) of the 304 chicks banded from 1987 to 2002 were followed to their first reproductive attempt (i.e., were recorded with eggs or chicks) at 25 natal sites (Table 1). Males and females as first breeders nested at a mean distance of 5.9 ± 6.3 km ($n = 36$) and 9.6 ± 10.2 km ($n = 37$) from their natal sites, respectively. Females dispersed significantly farther than males ($t = 2.14$, $P = 0.03$) and the ranges of their dispersal distances were dissimilar with males dispersing 0.7 to 28.0 km and females 1.0 to 46.2 km (Fig. 3). Natal dispersal distances of females by age groups were significantly greater than for males (Wilcoxon Test, $Z = -2.394$, $P = 0.003$; Table 2). Mean distance of females and males from natal areas to breeding territories decreased with age of first reproductive attempt (two-way ANOVA: $F = 11.381$, df = 4, $P = 0.019$).

Direction of Natal Dispersal.—There was a significant directional pattern to natal dispersal for males and females, based on directions to final locations for individuals. Mean final direction was not random for both cohorts, and we pooled all cohorts for estimation of overall mean direction ($\mu = 185.6°$, $\check{s} = 86.1°$; Fig. 4). Most individuals dispersed southeast from natal sites, suggesting that dispersal movements of individual ibis were significantly concentrated around the mean direction (Rayleigh's z; all $P < 0.05$).

Age of First Breeding.—There were 73 birds for which age of first breeding was precisely known from observations of courtship displays of marked individuals. The youngest birds participating in breeding were 2 years of age. The oldest bird recorded as a first breeder was 7 years of age. The range of ages of first reproduction was 2 to 6 years for females and 2 to 7 years for males (Fig. 5). The mean age of these birds when first recorded breeding was 3.89 ± 1.40 years ($n = 73$). First reproduction by females was not significantly earlier than males (females 3.64 ± 1.36 years, $n = 37$; males 4.17 ± 1.47 years, $n = 36$, $t = 1.60$, $P = 0.11$).

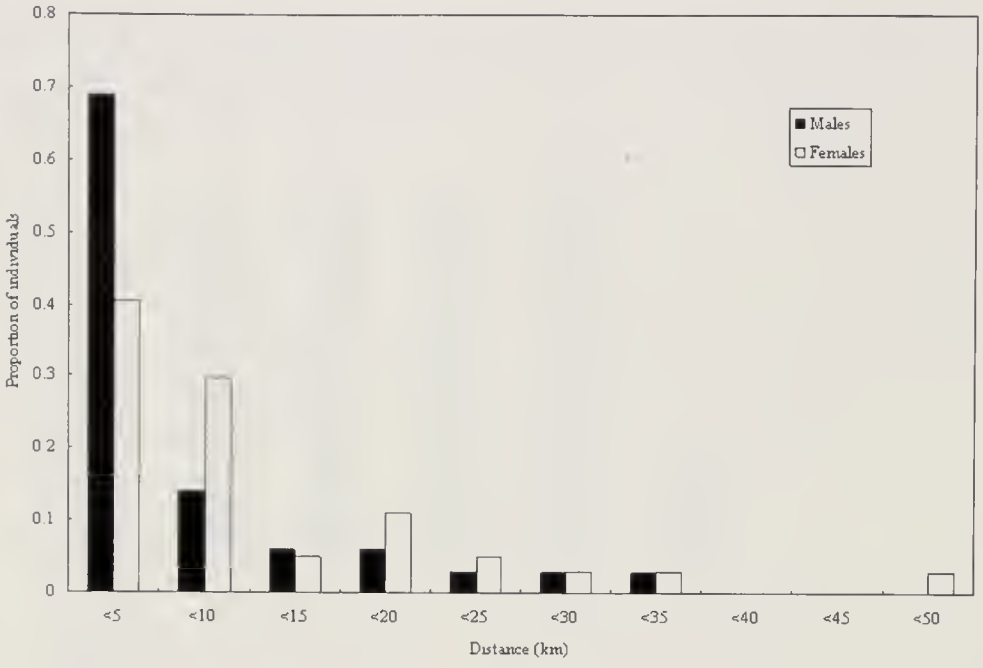

FIG. 3. Distribution of natal dispersal distances for Crested Ibis (n = 36 males and 37 females).

DISCUSSION

Measuring dispersal in spatially heterogeneous environments is essential for testing population dynamics models (Kareiva 1990), but obtaining unbiased dispersal data is difficult, because long-distance dispersers often go undetected (Koenig et al. 2000). We were able to track 73 individual ibis until they settled and paired, and our study areas were sufficiently large (~3,000 km^2) to allow reasonable quantification of long-distance dispersal (up to 50 km, Fig. 1). Multi-year observations allowed for large sample sizes for juveniles.

Crested Ibises had a skewed dispersal pattern with many individuals dispersing relatively short distances, but with some dispersing much greater distances (Fig. 3). Breeding territories are typically small with a diameter of 50–100 m (Shi and Cao 2001) with several nests on the same tree (Liu et al. 2003). However, all marked individuals dispersed from their natal home ranges (100% dispersed ≥0.7 km). A similar pattern has been reported for other Ciconiiformes, including Snowy Egrets (*Egretta thula*), Black-crowned Night Herons (*Nycticorax nycticorax*), and Forster's (*Sterna forsteri*) and Caspian terns (*S. caspia*), in contrast to Great Blue Herons (*Ardea herodias*) which have a tendency to return to natal areas to breed as adults (Gill and Richard 1979).

Gender-biased dispersal is common among many bird species with females usually dispersing farthest (Greenwood 1980). Females settled farther from natal sites than males in some Ciconiiformes such as White Storks (*Ciconia ciconia*) (Chernetsov et al. 2006), but it is most often the female that is more likely to leave the natal area and travel longer distances before settling to breed (Clarke et al. 1997). Our study strengthens the conclusions drawn by Greenwood (1980) regarding this broad, general pattern (Fig. 3).

TABLE 2. Natal dispersal distances (km) in relation to age and gender of Crested Ibis.

Parameter	Age of first reproduction ($\bar{x}$ ± SD)					
	2-yr	3-yr	4-yr	5-yr	6-yr	7-yr
Males	15.2 ± 9.7	7.3 ± 5.1	3.9 ± 2.4	3.7 ± 2.3	2.0 ± 0.3	2.6 ± 2.2
	(n = 4)	(n = 12)	(n = 8)	(n = 5)	(n = 3)	(n = 4)
Females	14.1 ± 10.2	12.2 ± 5.5	9.4 ± 6.3	7.4 ± 2.7	4.3 ± 1.9	0
	(n = 9)	(n = 9)	(n = 9)	(n = 6)	(n = 4)	(n = 0)
Gender combined	14.3 ± 9.9	9.4 ± 10.4	6.6 ± 7.4	3.9 ± 2.6	2.8 ± 1.6	2.6 ± 2.2
	(n = 13)	(n = 21)	(n = 17)	(n = 11)	(n = 7)	(n = 4)

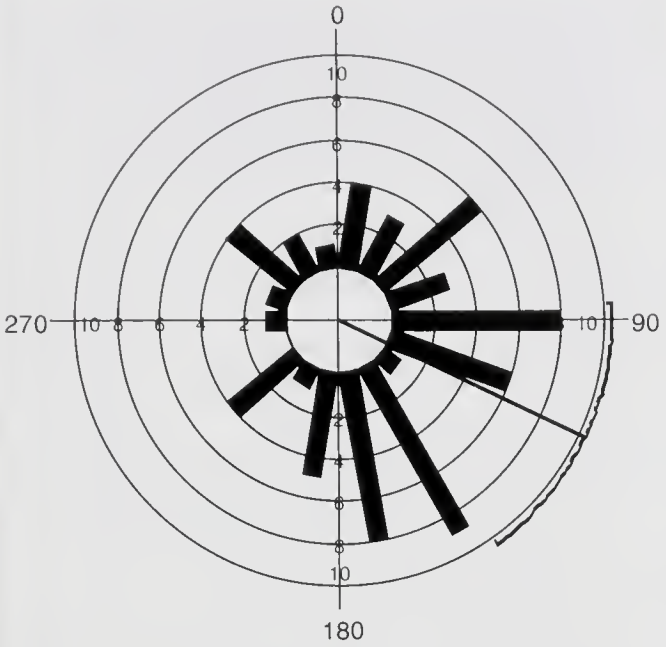

FIG. 4. Graphical depiction showing final direction from the natal site to first breeding territory for 73 banded Crested Ibis. Directions are spatially nonrandom (Rayleigh's z: all $P < 0.05$).

Direction of natal dispersal and post-fledging movement was likely in response to habitat factors. Crested Ibis were once commonly seen in towns and cities in agricultural areas, near which they could find large trees for nesting and suitable wetlands for feeding (La Touche 1934). The wild population that survived in Yangxian County persisted in remote mountainous districts at an altitude of 1,200 m, where human exploitation was not as severe as in neighboring areas (Shi et al. 1989, Shi and Cao 2001). The species has showed a recent preference to move to lower areas for breeding (Ding 2004). Crested Ibis prior to 1990 usually nested on oaks in mountainous areas above 1,000 m. They have colonized new nesting sites in recent years where they usually nest on pines at lower altitudes (700–900 m), presumably indicating the relict population had become confined to suboptimal upland habitat but is now expanding into more typical lowland areas. More recently, a few birds have been found breeding in patches of secondary forests close to human settlements (Liu et al. 2003).

Forty-nine (67.1%) of 73 marked chicks in our study required 2 to 4 years to become territorial (Fig. 5). Females bred no more than 1 year earlier than males on average, similar to Marabou Storks (*Leptoptilos crumeniferus*) (Pomeroy 1978), Scarlet Ibis (*Eudocimus ruber*), and Eurasian Spoonbill (*Platalea leucorodia*) (Hancock et al. 1992). These data may indicate the habitat is saturated or reflect other breeding constraints on the population. Variation in age of first breeding could reflect individual variation in physical condition or foraging skills or, alternatively, individuals selecting different strategies for maximizing reproductive success (Nelson 1977, Osorio-Beristain and Drummond 1993). Males are at least 1 year older than females in most pairs (Lu et al. 1997), and males were observed to have a dominant role in territory defense (Shi and Cao 2001). This suggests that greater experience is necessary for males to have a mate and hold a territory.

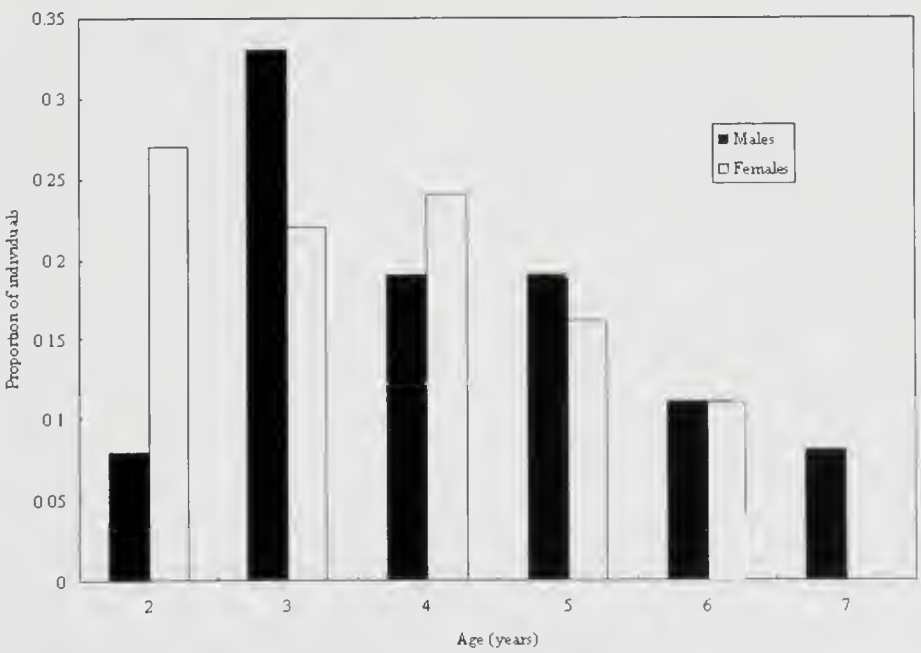

FIG. 5. Age of first breeding attempt (n = 36 males and 37 females).

Survival, productivity, and dispersal data are important parameters in population models that highlight stages in a species' life cycle where conservation actions may be most critical. Limited data on dispersal of both young and yearling ibis led to imprecise survival estimates, and the low success of first breeding attempts for each age class (Yu et al. 2006) suggest low year-to-year survival of juveniles. Our results indicate that young individuals are likely to disperse farther than adults, and females breed nearly 1 year earlier than males. The current distribution is progressively expanding to areas at lower elevation and denser human populations by dispersal of young individuals. These findings have potentially important implications for reintroduction programs that are currently being considered (Yu et al. 2009). We strongly recommend that reintroduction programs be conducted with younger (2–3 yrs of age) individuals which are more prone to establishing new territories and have low site fidelity.

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MORPHOLOGICAL AND GENETIC VARIATION BETWEEN MIGRATORY AND NON-MIGRATORY TROPICAL KINGBIRDS DURING SPRING MIGRATION IN CENTRAL SOUTH AMERICA

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ABSTRACT.—We attempted to distinguish spring passage migrant Tropical Kingbirds (*Tyrannus melancholicus*) from resident conspecifics where they overlap in South America. Migrant males at our Bolivian study site had significantly less tail feather molt and longer wing chords than resident males. Migrant females had significantly longer wing chords, less flight feather molt, and less flight feather wear than resident females. We found no evidence of genetic population differentiation between migrants and residents. We also compared wing chords of migrants and residents to those of breeding kingbirds in breeding populations further south. Wing chords of migrants were more similar to those of breeders from further south than to those of breeders at our study site. An ability to distinguish migrant from resident conspecifics will be critical to understanding migrant winter ecology, migratory routes, and connectivity of migratory populations in South America. *Received 18 May 2009. Accepted 2 December 2009.*

Almost 70% of neotropical austral migrant species (hereafter "austral migrants"), which migrate wholly within South America, are characterized by having both migratory and non-migratory (permanent resident) populations (Stotz et al. 1996). Populations of permanent residents usually occur within or close to tropical latitudes, whereas populations of migratory individuals occur in temperate latitudes during the breeding season and in tropical latitudes during the non-breeding season. Ranges of migratory and resident populations of austral migrants typically overlap during the non-breeding season. Patterns of migration within the range of overlap are rarely documented because distinguishing between migratory and resident individuals is difficult. Thus, for the great majority of austral migrants, we know little about migratory routes, non-breeding season ecology, population connectivity, and intraspecific interactions between residents and migrants.

Zimmer (1938) and Lanyon (1978) used seasonal distribution, morphology, and molt data to study where non-breeding populations of migrants and residents overlap in South America. More recently, Chesser (1995, 1997) primarily used seasonal distribution data to identify the range of winter overlap of migrant and resident austral migrant populations at the center of the continent. Significant morphological differences in other migratory systems exist between migrant and resident individuals of the same species; those differences have been used to distinguish between co-occurring migrants and residents. For example, migratory European Blackcaps (*Sylvia atricapilla*) have longer, more pointed wings and smaller bodies than resident conspecifics in Iberia (Tellería and Carbonell 1999), allowing accurate classification of migrant and resident Blackcaps in winter (Pérez-Tris et al. 1999). Similarly, a migratory subspecies of Common Reed Bunting (*Emberiza schoeniclus*) in Spain has larger and more convex wings than a sedentary subspecies (Copete et al. 1999). Molt schedules may also differ between co-occurring resident and migrant individuals (Lundberg and Eriksson 1984).

Range overlap of resident and austral migrant populations in the non-breeding season occurs for Tropical Kingbirds (*Tyrannus melancholicus*), which are permanent residents in most of tropical South America. Two subspecies (*satrapa* and *despotes*) appear to be permanent residents in northern Amazonia (Traylor 1979, Chesser 1995), whereas the subspecies *melancholicus* is a resident from most of Amazonia south to ~18° S. South of this latitude, *melancholicus* occurs only in summer, migrating north after breeding into the range of permanent resident populations (Chesser 1995; Fig. 1).

We studied a resident population of Tropical Kingbirds (hereafter "kingbirds") at a site in

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FIG. 1. Distribution of the nominate subspecies of Tropical Kingbird (*Tyrannus m. melancholicus*) in South America. Gray polygon represents the permanent distribution of the species and the hatched polygon south of 18° S represents the seasonal breeding range. Star represents location of Caparú Biological Station, Bolivia. Adapted from Chesser (1995).

eastern Bolivia (~15° S) within the range of the nominate subspecies. We noticed that many kingbirds captured during September and October were much fatter than others, and that fewer of those fat individuals were seen again at the site, compared to those individuals that were less fat. We hypothesized that fatter individuals were passage migrants, on their way to breeding areas further south. Our objective was to assess different methods of distinguishing between migrant and resident kingbirds where they co-occur. We compared: (1) the molt schedule, wing chord, and genetic signature between putative migrants and residents, and (2) the wing chord of migrants and residents at the study site with wing chords of kingbirds breeding further south.

METHODS

Study Site and Field Procedures.—Our study site was Caparú Biological Station (CBS), Department of Santa Cruz, eastern Bolivia (14° 49′ S, 61° 11′ W; 170 m asl). The site is near the center of the continent, north of the boundary of migratory kingbirds' breeding range and south of a large expanse of potential wintering area (i.e., Amazonia; Fig. 1). The habitat is primarily cerrado grassland, humid forest edge, and cattle pasture. Kingbirds were captured using nylon and polyester mist nets (12 or 18 m × 2.6 m, 36 or 38 mm mesh size) where they were most abundant (e.g., ponds and forest edge). Kingbirds were also banded as nestlings and parents were captured at their nest by placing a stuffed Purplish Jay (*Cyanocorax cyanomelas*), a common nest predator, nearby.

Kingbirds were banded with uniquely-numbered aluminum bands provided by the Museo de Historia Natural Noel Kempff Mercado (MHNNKM), Santa Cruz, Bolivia as well as with up to three celluloid color bands. Banding was conducted during most months from October 2004 to July 2007. Data recorded for captured kingbirds included reproductive condition (presence/absence of cloacal protuberance or brood patch), fat score (measured on an 8-point scale), body molt (measured on a 5-point scale), primary feather wear (measured on a 6-point scale), length of unflattened wing chord, tail, beak, and tarsus length, and mass (Ralph et al. 1993, Pyle 1997). We classified flight feather and tail molt as present or absent; molt was classified as "present" if at least one secondary or primary feather or retrix was molting. These measurements were taken by AEJ and AMM, who collected data together on a regular basis to minimize observer error. We classified birds in their first year of life as hatch-year individuals (HY) or after-hatch-year individuals (AHY) for individuals that were of unknown age but at least 1 year of age. Each year began on 1 September because the kingbird breeding season lasts from mid-September to February.

Blood was taken for genetic analysis from all color-banded individuals by piercing the brachial vein with a sterile needle. Blood was collected in a 0.5-mL heparinized capillary tube and stored in DNA lysis buffer (Seutin et al. 1991). We assigned gender of live birds based upon primary notch length (Pyle 1997) and, when necessary, through molecular methods using primers 2550F and 2718R (Fridolfsson and Ellegren 1999). Optimal cycle conditions were 95° C for 5 min, 95° C for 30 sec, an annealing temperature of 50° C for 1 min, and 72° C for 45 sec, repeated 39X, and held at 72° C for 10 min, using 15 µL Mg. Blood samples were deposited at the MHNNKM.

We documented seasonal presence/absence of color-banded kingbirds after banding to identify

which individuals were residents. We divided the ~700-ha study site into 23 sampling plots and methodically searched for banded individuals in each plot at least once/month throughout most of the annual cycle. These censuses were completed from February 2005 to August 2007. We did not visit plots during most of the non-breeding season of 2005 because we were absent during June–September. We also visited plots on 28 January to 12 February, 2–19 March, and 15–27 June 2008. We geo-referenced the location when a color-banded individual was observed using a Global Positioning System receiver (Garmin GPS 76, Olathe, KS, USA), noting the date, time, and color band combination.

AEJ measured 120 kingbird skins from Argentina and Paraguay housed at Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN; Buenos Aires, Argentina) and 79 skins at Louisiana State Museum of Natural Science (LSUMZ; Baton Rouge, USA) to examine whether morphological variation among populations could be useful in identifying breeding locations of passage migrants at CBS. BF also measured 60 study skins from Paraguay and Argentina at the American Museum of Natural History (AMNH; New York City, USA). Unflattened wing chord was measured as on live kingbirds at CBS, following Ralph et al. (1993). Wing chord was not measured on specimens with excessively worn primary feather tips. We previously standardized our measurements to minimize inter-observer measurement error.

We isolated DNA from blood samples using the PUREGENE DNA Purification Kit (Gentra Systems, Minneapolis, MN, USA) and reviewed the literature to identify potential primers of polymorphic loci developed from related species in Tyrannidae. Six microsatellite primers were successfully optimized from *Empidonax* (GATA5; Pearson et al. 2006) and *Sayornis* (SAP22, SAP32, SAP47, SAP50, SAP156; Watson et al. 2002, Beheler et al. 2007). Optimal PCR cycling conditions for all primers were: 95° C for 4 min followed by 94° C for 1 min, then 55° C for 1 min, and 72° C for 1 min, repeating the last three steps 35X with a final cycle of 72° C for 10 min. We used 12.5 μL of master mix for all primers, 800 μM dNTP's, 2.5 μM $MgCl_2$, 0.26 μM of each primer, and a concentration of 10–20 ng of sample DNA.

We combined males and females for genotyping due to low sample sizes of kingbirds of known gender for which we had DNA available for analysis. We analyzed DNA from 15 migrants and 15 residents. DNA was run on an ABI 3730XL, 96 capillary automated sequencer (Biosystems, Foster City, CA, USA). The program GENEMAPPER (Softgenetics, State College, PA, USA) was used to score the alleles. Population structure was tested in program STRUCTURE 2.2 (Pritchard et al. 2000) assuming a model of admixture, correlated allele frequencies, and K = 1 to 2 (where K is the number of populations) with 10 independent replicates for each K (length of the run 1,000,000 MCMC re-samples), and 100,000 burn-in. We used program ARLEQUIN 3.01 (Excoffier et al. 2005) to test for departures from Hardy-Weinberg equilibrium, and to calculate the amount of linkage disequilibrium between pairs of loci. Bonferroni correction was applied for multiple comparisons in both tests. There was violation of Hardy-Weinberg equilibrium in one locus (SAP32) for both resident and migrant populations, and in only migrants for another locus (SAP50) but, overall, loci adhered to equilibrium. Population differentiation was tested by performing a hierarchical analysis of molecular variance (AMOVA) to calculate global and pairwise F_{st} in ARLEQUIN 3.01.

We only consider adult kingbirds (i.e., those with only trace juvenile plumage or 95% or more of the skull ossified) to avoid potential confounding effects of age with wing chord (Low 2006), fat content (e.g., Lundberg 1985), and molt (e.g., Debruyne et al. 2006). After-hatch-year (AHY) kingbirds captured in September and October that had higher subcutaneous lipid scores (i.e., ≥6 on an 8-point scale, *sensu* Ralph et al. 1993) were re-observed significantly less often than those with lower lipid scores (i.e., <6 on the same scale; Fig. 2). This was true of both males ($\chi^2 = 11.8$, $P = 0.001$) and females ($\chi^2 = 7.1$, $P = 0.008$). We classified as passage migrants all AHY kingbirds captured in September or October with lipid scores of 6 or higher, that were not re-observed after being color banded, and which had no incubation patch or cloacal protuberance (to exclude the possibility they were breeding at the study site). We classified residents as individuals that were captured in September or October, had subcutaneous lipid scores of 1–5, and re-observed at least once later on the study site. There were insufficient residents for which DNA was available for analyses, and we included as residents for purposes of DNA analyses individuals with the

FIG. 2. Relationship between amount of subcutaneous fat and frequency of being re-observed for AHY Tropical Kingbirds color banded during spring migration at Caparú Biological Station, Bolivia; "Low" = subcutaneous fat score of <6 on an 8-point scale, "High" = subcutaneous fat score ≥6.

same characteristics captured in November, which is well into the breeding season (A. E. Jahn, unpubl. data).

RESULTS

Resident Tropical Kingbirds at CBS tended to molt during and after the breeding season (Fig. 3). Spring passage migrants had significantly less flight feather molt (Kruskal-Wallis $\chi^2 = 5.96$, $P = 0.015$, $n = 81$) and significantly less tail molt (Kruskal-Wallis $\chi^2 = 7.66$, $P = 0.006$, $n = 79$) than residents when data for males and females, and those of unknown gender were combined. However, there was no significant difference between migrants and residents in body molt (Kruskal-Wallis $\chi^2 = 1.07$, $P = 0.30$, $n = 81$). Migrants also had less primary feather wear (Kruskal-Wallis $\chi^2 = 10.36$, $P = 0.001$, $n = 80$) and longer wings ($t = 4.17$, $P < 0.0001$, $n = 79$) than residents.

Female passage migrants had significantly less flight feather molt, less primary feather wear, and longer wings than resident females (Table 1). Male residents had significantly more tail molt than male migrants, but there was no significant difference in flight feather molt or primary feather wear between migrant and resident males. Male migrants were also characterized by a significantly longer wing chord than male residents (Table 1).

We used discriminant function analysis (DFA) to examine the level at which we could correctly classify migrants and residents at the site during spring migration. We combined data for males and females due to the relatively low sample sizes for each. We first examined which of the five morphological measurements (flight feather molt, tail molt, primary feather wear, body feather molt, and wing chord) provided the most explanatory power within the discriminant function. A test of the equality of group means revealed that body molt contributed the least amount of explanatory power to the discriminant function ($F_{1,72} = 1.09$, $P = 0.30$); we therefore excluded it from further analysis. All four remaining variables significantly contributed to the discriminant function and were retained in the full model. The parameter with the least explanatory power was flight feather molt ($F_{1,72} = 4.48$, $P = 0.038$), and the parameter with the highest explanatory power was wing chord ($F_{1,72} = 16.84$, $P < 0.0001$). The resulting DFA correctly classified 86.0% of migrants and 71.0% of residents with an overall success rate of 79.7%.

Wing chord from study skins of males at >18° S ($n = 146$) was significantly longer than that of both resident ($t = -6.93$, $P < 0.0001$, $n = 15$) and passage migrant males at the study site ($t = -2.71$, $P = 0.007$, $n = 21$; Fig. 4). Wing chord

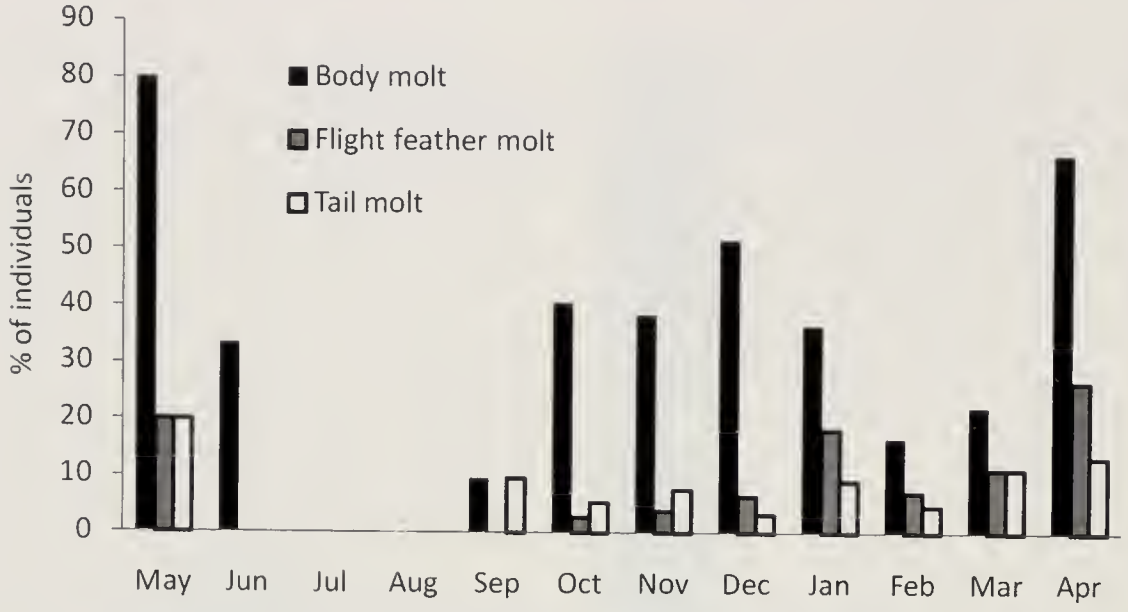

FIG. 3. Molt schedule of AHY color-marked, re-observed resident Tropical Kingbirds at Caparú Biological Station, Bolivia. Data represent the percentage of kingbirds per month with each molt type. Percentages may not sum to 100 because individuals can have more than one molt type.

from study skins of females at >18° S (n = 83) was significantly longer than that of female residents (t = 6.787, P < 0.0001, n = 11) but not of female passage migrants at the study site (t = 1.055, P = 0.29, n = 16; Fig. 4).

We found better support using genetic data for the presence of one population (log likelihood = −515.2) than for the presence of two populations (log likelihood = −516.6), based on Bayesian analyses of population structure, as implemented in program STRUCTURE 2.2. This suggests there is no significant genetic structure between migrant and resident kingbirds in the six loci tested. AMOVA also gave no indication of genetic differentiation between migrants and residents (F_{st} = 0.01576, P = 0.578). There was no indication of departures from Hardy-Weinberg equilibrium or of linkage disequilibrium (Table 2).

We conducted DFA for migrants and residents classified as above, but without considering re-observation data (i.e., using only fat scores) to check whether using fat content alone to distinguish between migrants and residents is as useful

TABLE 1. Morphological and molt comparisons of resident and passage migrant Tropical Kingbirds at Caparú Biological Station, Bolivia. Values for flight feather and tail molt are percent of migrants and residents with molt present. Values for body feather molt and primary feather wear represent mean score on a 5- and a 6-point scale, respectively (high scores indicate more molt or wear).

	Residents (n)	Migrants (n)	Test statistic	P
Males				
Flight feather molt	12% (17)	0% (21)	2.54[a]	0.111
Tail molt	20% (15)	0% (21)	4.46[a]	0.035
Body feather molt	2.44 ± 1.09 (16)	2.24 ± 1.18 (21)	0.28[a]	0.595
Primary feather wear	2.06 ± 0.25 (16)	1.86 ± 0.48 (21)	2.42[a]	0.120
Wing chord, mm	111.27 ± 2.87 (15)	113.9 ± 2.84 (21)	2.735[b]	0.010
Females				
Flight feather molt	25% (12)	0% (16)	4.06[a]	0.044
Tail molt	8% (12)	0% (16)	1.25[a]	0.264
Body feather molt	2.82 ± 0.98 (11)	2.47 ± 1.19 (15)	0.50[a]	0.481
Primary feather wear	2.58 ± 0.79 (12)	1.80 ± 0.56 (15)	6.92[a]	0.009
Wing chord, mm	106.09 ± 1.97 (11)	110.63 ± 2.63 (16)	4.846[b]	<0.0001

[a] Kruskal-Wallis test.
[b] Independent samples t-test.

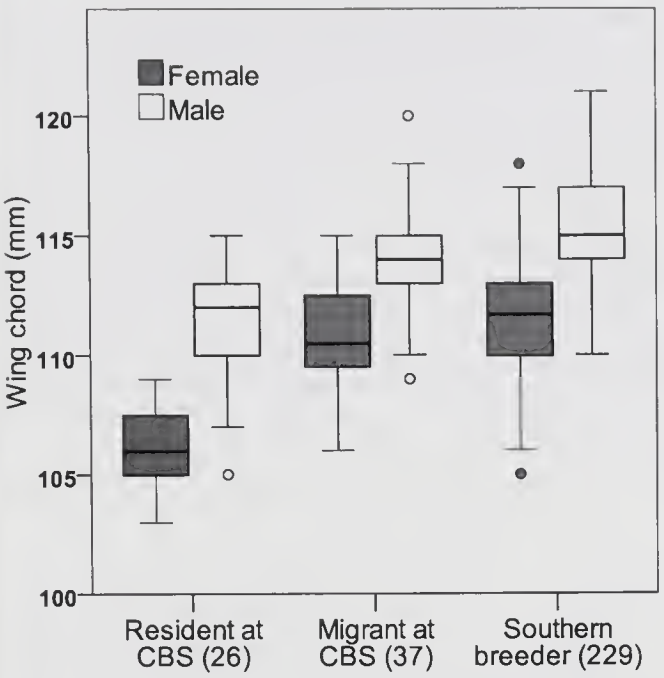

FIG. 4. Box-and-whisker diagram depicting wing chord of Tropical Kingbird residents, passage migrants, and breeders from seasonal breeding range south of 18° S latitude in South America. Numbers in parentheses on x-axis labels represent sample sizes. Rectangles depict the range of the first to third quartiles and the dark horizontal line within each rectangle depicts the median. Lines from each rectangle extend to the larger and smaller values, and circles outside of rectangles represent outliers.

as using fat plus re-observation data. Body molt within the revised DFA had practically no explanatory power ($F_{1,153} = 0.01$, $P = 0.94$) and was excluded. The resulting test of equality of group means revealed that flight feather molt had the most explanatory power ($F_{1,159} = 4.10$, $P = 0.044$) and that wing chord had the least ($F_{1,159} = 0.28$, $P = 0.60$). The DFA correctly classified 75% of migrants and 26.5% of residents with an overall success of 41.0%.

DISCUSSION

Tropical Kingbirds with high lipid scores and those that were not re-observed after banding (i.e., putative migrants) were characterized by traits typical of migrants in the Northern Hemisphere: advanced molt schedules (Lundberg and Eriksson 1984) and longer wings (Haberman et al. 1991, Tellería and Carbonell 1999, Milá et al. 2008) relative to kingbirds with less fat and which were re-observed at the site (i.e., residents). The differences between the two groups in molt, feather wear, and wing chord from our site at the middle of the continent, where passage migrants would be expected to occur if migrating between low latitudes to the north and temperate breeding areas to the south, strongly suggest some Tropical Kingbirds are long-distance migrants that overwinter in central or northern Amazonia.

Migrant females at CBS had wing chords similar to breeders from the seasonal breeding range >18° S, whereas male migrants had significantly shorter wings than kingbirds from the seasonal breeding range. Thus, at least some female spring passage migrants were likely returning to the seasonal breeding range, while male migrants may have been returning to the seasonal breeding range, as well as to latitudes closer to the study site. Future research on geographical variation in wing chord and genetic structure south of the study site may reveal geographical variation in traits that could be useful in identifying the breeding location of these migrants.

Molt of resident kingbirds at CBS tended to occur primarily just before, during, and after the breeding season (Oct–Dec). Thus, many resident kingbirds at CBS likely had not molted prior to passage of spring migrants. Passage migrant male kingbirds had a more advanced pre-alternate tail molt compared to local resident males, and female migrants had a significantly more advanced flight feather molt than residents at CBS. This indicates migratory kingbirds have more advanced pre-alternate molt schedules than non-migratory individuals at CBS. Lundberg and Eriksson (1984) found the post-juvenile molting period of migratory European Starlings (*Sturnus vulgaris*)

TABLE 2. Genetic diversity for resident and migrant Tropical Kingbirds. Genetic diversity parameters include mean observed heterozygosity (H_O), mean expected heterozygosity (H_E), inbreeding coefficient (F_{IS}) based on the average of six loci, average number of alleles per locus (A), and average number of private alleles (PA).

	H_O–H_E	F_{IS}	Average gene diversity across loci	A	PA	n
Residents	0.423–0.478	0.020 ($P = 0.497$)	0.422 ± 0.259	6.67	1.8	15
Passage migrants	0.438–0.611	0.107 ($P = 0.088$)	0.582 ± 0.339	8.00	3.0	15

was shortened relative to that of non-migratory individuals with migrants finishing the molt of primary and secondary feathers significantly earlier than residents. They postulated the shortened molting period of migrants was constrained by the need to migrate after breeding. Our study focused on spring migration and we do not know if migrants molt their feathers in a shorter span of time compared to residents. That migrant kingbirds finish the pre-alternate molt earlier than resident kingbirds suggests migration can be a constraint on molt timing. It remains unknown whether migration constrains the scheduling of molt at tropical latitudes.

Genetic analysis revealed no significant population subdivision between migrant and resident Tropical Kingbirds. The lack of microsatellite structure in our study may be due to at least three reasons: (1) too few individuals or loci sampled, (2) relatively high gene flow occurring among populations, and (3) recent colonization of southern latitudes by kingbirds.

Our results corroborate previous evidence that populations of Tropical Kingbirds breeding at high southern latitudes in South America (i.e., *T. m. melancholicus*) have longer wing chords than populations breeding closer to the equator (i.e., *T. m. satrapa* and *T. m. despotes*; Cory and Hellmayr 1927). Likewise, southern breeding populations of Swainson's Flycatcher (*Myiarchus swainsoni*) in South America have longer wing chords than populations breeding at tropical latitudes (Lanyon 1978, Joseph et al. 2003).

Distinguishing between migrant and resident conspecifics when they occur together at tropical latitudes is important in advancing our understanding of the evolution of migratory behavior. However, migrants may not be obviously different in morphology from permanent resident individuals in most species of austral migrants because austral migrants that overwinter in South America's tropics migrate an average of 9.2° (±8.5) latitude (Chesser 1994).

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RED-COCKADED WOODPECKER MALE/FEMALE FORAGING DIFFERENCES IN YOUNG FOREST STANDS

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ABSTRACT.—The Red-cockaded Woodpecker (*Picoides borealis*) is an endangered species endemic to pine (*Pinus* spp.) forests of the southeastern United States. I examined Red-cockaded Woodpecker foraging behavior to learn if there were male/female differences at the Savannah River Site, South Carolina. The study was conducted in largely young forest stands (<50 years of age) in contrast to earlier foraging behavior studies that focused on more mature forest. The Red-cockaded Woodpecker at the Savannah River site is intensively managed including monitoring, translocation, and installation of artificial cavity inserts for roosting and nesting. Over a 3-year period, 6,407 foraging observations covering seven woodpecker family groups were recorded during all seasons of the year and all times of day. The most striking differences occurred in foraging method (males usually scaled [45% of observations] and females mostly probed [47%]), substrate used (females had a stronger preference [93%] for the trunk than males [79%]), and foraging height from the ground (mean ± SE foraging height was higher for males [11.1 ± 0.5 m] than females [9.8 ± 0.5 m]). Niche overlap between males and females was lowest for substrate (85.6%) and foraging height (87.8%), and highest for tree species (99.0%), tree condition (98.3%), and tree height (96.4%). Both males and females preferred to forage in older, large pine trees. The habitat available at the Savannah River Site was considerably younger than at most other locations, but the pattern of male/female habitat partitioning observed was similar to that documented elsewhere within the range attesting to the species' ability to adjust behaviorally. *Received 24 March 2009. Accepted 9 November 2009.*

The Red-cockaded Woodpecker (*Picoides borealis*), endemic to the pine (*Pinus* spp.) forests of the southeastern United States, is strongly associated with open, mature longleaf pine (*P. palustris*) forest (USFWS 2003). Historically, this preferred habitat has been maintained by fire without which the hardwood midstory may develop to make the area unsuitable for Red-cockaded Woodpeckers. A reduction in the frequency of fire (Jackson 1986, Ligon et al. 1986, Walters 1990), loss of longleaf pine forests (Conner et al. 2001), and a general overall reduction in the age of forest stands resulting from short-rotation ages (Wahlenberg 1960, Frost 1993) have resulted in modification or loss of habitat throughout the geographic range of the species. Red-cockaded Woodpeckers are cooperative breeders living in social groups consisting of the mated pair and often one or more helpers, which are usually male and the offspring of one or both members of the breeding pair. They construct their own cavities in mature, living pine trees, which are used for nesting and night roosting (Jackson et al. 1979). This is a fairly long-lived species in which all individuals in the group cooperate in territorial defense, excavation of cavities, incubation, and feeding nestlings and fledglings (Hooper and Lennartz 1981). There is a long period of juvenile dependency, which Ligon (1968) speculated was the result of the young having to learn specialized foraging techniques.

The Red-cockaded Woodpecker population at the Savannah River Site (SRS), South Carolina, had declined to a low of four individuals by 1986 at which time an intensive management effort was initiated to prevent extirpation of the species at the site. Results and details of the management program that was implemented are available in Franzreb (1997). Most forest stands on the site had been replanted with pine species when this study was initiated in 1992 and ~92% of the pines were ≤40 years of age (K. E. Franzreb, unpubl. data). Previous Red-cockaded Woodpecker studies on foraging and habitat use relied on areas that contained a fairly large proportion of older trees in contrast to the younger age and smaller size-class distribution patterns for trees at SRS where old, large diameter trees were sparse.

The Red-cockaded Woodpecker population at SRS is intensively managed including: removal of nest site competitors such as southern flying squirrels (*Glaucomys volans*) from cavities; translocations of woodpeckers from off-site locations to augment the population; translocations on-site to replace lost mates or establish new pairs; and research to examine habitat requirements, home-range size and configuration, and foraging behavior. All birds were monitored, nestlings were banded, and the reproductive rate was estimated for each group on an annual basis (Franzreb 1997). The Red-cockaded Woodpecker

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population increased on the site during the course of this study from 36 to 89 birds, including 21 translocated birds from off-site (Franzreb 1997, 1999).

Previous investigations by others were conducted in habitat largely consisting of stands with relatively mature trees, offering a more structurally complex vegetative environment with greater opportunities to partition the habitat than likely found in much younger forest stands. Further, most studies of Red-cockaded Woodpecker foraging behavior and habitat use have not differentiated observations by males and females; those that did noted differences in foraging behavior. Published studies have noted male/female variation in method of foraging, tree species selection, use of hardwoods, foraging height from the ground, foraging substrate, tree height selection, location, and tree condition (Skorupa 1979, Hooper and Lennartz 1981, Rudolph et al. 2007). However, Zwicker and Walters (1999) found no difference in foraging in relation to tree age, diameter at breast height, or species between male and female Red-cockaded Woodpeckers in the Coastal Plain of North Carolina. Porter and Labisky (1986) suggest that differing foraging requirements in different habitats necessitate habitat-specific forest management guidelines for Red-cockaded Woodpeckers.

The objectives of my study were to: (1) examine habitat partitioning between foraging male and female Red-cockaded Woodpeckers in a habitat that largely consisted of stands of trees that were considerably younger than most habitat found elsewhere in the range; (2) compare habitat availability with foraging use for males and females; (3) assess differences among groups in selection and preferences on the SRS; and (4) discuss the possible role younger forest stands may have in the range-wide management and conservation of the species.

METHODS

Study Area.—The Savannah River Site, a National Environmental Research Park, is in the Upper Coastal Plain Physiographic Region in Aiken, Allendale, and Barnwell counties, South Carolina, USA. Most of the land was acquired by the Department of Energy (DOE) in the late 1940s and early 1950s to develop into a nuclear production facility. Most of the site was in agricultural use or recently had been harvested for timber prior to acquisition by DOE. The USDA, Forest Service has managed the natural resources of the site for DOE since 1952. The area managed for woodpeckers during this study contained 31,970 ha of pine forest consisting of longleaf (37.7% of the pine), loblolly (*P. taeda*, 45.4%), slash (*P. elliottii*, 13.4%), and other pines (0.2%), in addition to pine-hardwoods (3.3%) (Glenn Gaines, U.S. Forest Service, unpubl. data). Most of the existing pine stands are the result of replanting efforts undertaken in the 1950s, although there are some residual older pine trees. Approximately 92% of the pine trees were ≤40 years of age (K. E. Franzreb, unpubl. data).

Foraging Data Collection.—Each Red-cockaded Woodpecker on the site was banded with a unique set of colored plastic leg bands for field identification and also with a numbered aluminum leg band provided by the U.S. Geological Survey. I obtained the necessary endangered species permits and banding permits from the U.S. Fish and Wildlife Service, U.S. Geological Survey, and State of South Carolina.

I selected seven groups of Red-cockaded Woodpeckers for observation on SRS based largely on their history of successfully breeding, increasing the likelihood the group would be present for the entire length of the study. Each group consisted of a breeding male and breeding female and often at least one helper. There was no turnover in either member of the breeding pair for two groups (groups 3 and 6). The male breeder also remained the same for three of the other groups (groups 1, 4, and 7). The breeding female varied from a group that had no turnover during the study, to changing every breeding season (group 2). Group composition during most years included at least one helper and there was no group that did not have a helper at least one of the years. The Red-cockaded Woodpecker population on the site during this study increased from 36 to 89 birds, including 21 translocated individuals from off-site (Franzreb 1997, 1999).

Foraging observations were obtained from 5 May 1992 to 26 July 1995. Each foraging observation consisted of: individual identification (band colors), date, time, tree species, tree height (m), tree condition (alive or dead), diameter at breast height (dbh) (cm), tree age, foraging method, foraging substrate (trunk, live limb, dead limb, cone), foraging height from the ground (m), timber stand location (compartment and stand number), and weather conditions (percent cloud

cover, wind conditions, precipitation). Tree age, height, and dbh are likely to be positively correlated. These three variables are included because forest managers use them in developing management plans and there is a large amount of variation depending on site quality and physiographic region. The location of each observation was defined using a global positioning system (GPS) Trimble Pathfinder Professional (use of brand names conveys no recommendation by the U.S. Forest Service). Observations were obtained for all members of the Red-cockaded Woodpecker groups. Data were collected during all seasons of the year and all times during the day. Birds were observed from the time of leaving the roost cavity in the morning and, if possible, until they returned to the cavity at night. Each bird located was followed until it made a foraging "strike" (defined as an actual attempt to collect prey) at which time the first observation was taken. At least 15 min separated sequential observations of the same individual to minimize inter-dependence of subsequent observations (Hejl et al. 1990). Porter et al. (1985) reported that a 15-min interval between sequential observations was sufficient for independence for Red-cockaded Woodpeckers. I accounted for possible correlation among observations of the same individual instead of relying on the informal 15 min rule.

Vegetation Data.—I used the Continuous Inventory of Stand Conditions (CISC) data base for information on stands such as dominant tree vegetation, stand age, and stand condition on the SRS (U.S. Forest Service, unpubl. data). A stand is a contiguous group of trees sufficiently uniform in age-class distribution, composition, and structure growing on a site of sufficiently uniform quality to be a distinguishable unit (Helms 1998). More detailed information was obtained by sampling vegetation in all stands within 800 m of the nest tree of each of the Red-cockaded Woodpecker groups studied. Most foraging observations occurred within 800 m of the nest tree of each group. Hardwood and pine trees in each stand were sampled using 0.04-ha fixed-radius plots established along transect lines at a rate of one plot per 2 ha of stand size following James and Shugart (1970). The beginning of each transect in a stand was established from a random point. Sample stations were separated by 50 m and transects were at least 50 m apart. The following variables were measured in each 0.04-ha plot for every tree: tree species, tree height (m), tree condition (alive, dying, or dead), diameter at breast height (dbh) (cm), age (increment bore reading of 4,945 trees including 1,061 hardwoods and 3,884 pines or CISC for even-aged pine stands), location (compartment/stand/Red-cockaded Woodpecker group number), and specific plot location.

Statistical Analyses.—A randomized block experimental design was used with repeated observations where blocks are the Groups and treatment is Gender, which is tested with the Group*Gender interaction as the error term. Observations of each individual bird were represented as BirdID (individual band of a bird) and nested within each Group*Gender. This is equivalent to a randomized block repeated measures design where observations of a given bird follow a compound symmetry covariance matrix (common variance and common covariance). There were numerous observations of the same individual during the 3-year study period, often ranging to over 100 observations of certain individuals. I used Proc Mixed (SAS 2004) for analysis that considered nesting or clustering of repeated observations for a given bird. This weighted the observations of individual birds so those with high numbers of observations would not unduly influence the outcome and bias the results (Rao and Scott 1992). This ensured that error terms and variances would be calculated correctly, yielding valid tests of hypotheses. I obtained least-squares means (hereafter referred to as means) for all continuous variables (foraging height, tree height, tree dbh, and tree age) for males and females in each group and for all groups combined. I tested differences between means using an F-statistic based on the mixed model using Proc Mixed. Individuals with fewer than five observations over the 3-year period were deleted from the analysis, which affected the degrees of freedom. Groups with the highest number of observations tended to have the highest number of birds with observations of more than five and these groups had the largest degrees of freedom indicated by the denominator term. I examined each group separately as well as combining data for all males and for all females. The amount and distribution of the habitat described by the variables studied differed within the home ranges of each group. Comparisons of the data on a per group basis provide a more complete representation of the range of foraging behavioral differences for males and females.

I combined all observations of all pine trees regardless of species and then grouped them by age, height, and dbh class interval to allow for comparison of the distribution of observations for the continuous tree variables by gender. Tree height and foraging height data were grouped by 3-m intervals. Age class data were grouped into 10-year intervals. There were few observations in trees <30 years of age and the age class intervals <30 were grouped. Tree dbh data were grouped by 5-cm size class intervals. The distribution of observations of males versus females was compared for these variables as well as for the other categorical variables (method, substrate, tree species, and tree condition) using the *F*-statistic in the Rao-Scott modified likelihood ratio test as obtained from Proc SurveyFreq (SAS 2004) for each group, and for males and females of all groups combined. This considered the nesting of the repeated observations for a bird in much the same way as the mixed model did using Proc Mixed for the other continuous variables. The Rao-Scott modified likelihood ratio test uses the survey design to adjust the typical Pearson Chi-square test by dividing the *P*-value by the survey design effect. The *F*-statistic used is an additional modification that provides a better statistic as suggested by SAS (2004). Degrees of freedom varied depending on the number of categories compared. Any cells with fewer than five observations were merged for these tests with the closest adjoining cell until there were at least five observations. The clustering process in the Rao-Scott tests also affected degrees of freedom.

I examined tree composition within an 800-m radius circle with a group's nest tree as its center. The value of 800-m was selected because it was the same radius used by USFWS in its recommended foraging guidelines for this species. I estimated how many pine and hardwood trees of specific ages, heights, and dbh were available within each of these stands or portions thereof using the 0.04-ha plot vegetation information. I then estimated the availability of the resources (tree species, tree heights, dbh, and tree age) within the 800-m radius circle. These availability data were used to derive estimates of how many observations were expected to occur if birds were using the foraging resources randomly. ArcInfo coverages were used to aid in this process. The percent use by each gender in each Red-cockaded Woodpecker group of pine trees by tree species and by tree age, tree height, and dbh class intervals was compared to expected use based on availability of these trees within the 800-m radius circle. Males and females in each group, and all males versus all females combined were compared with respect to the distribution of actual observations versus the number of observations expected. Expected values were based on resource availability within 800 m of the nest tree and these comparisons were used to examine any preference or avoidance of foraging resources. Any cells that contained <5 observations were either deleted or grouped with similar cells so the overall number of observations in each cell was >5.

I compared means for tree age and dbh for each pine species for trees that were available in the habitat of each of the groups and overall for all groups combined using Proc GLM and the Bonferroni adjustment for multiple comparisons (SAS 2004). All *F*-tests and comparisons of means were performed at the 0.05 significance level. Values reported are means ± SE.

I used Levin's (1968) measure of niche breadth where $B = 1/\Sigma p^2_i$ and p_i is the proportion of observations recorded in class "*i*." I followed Schoener (1970) to estimate niche overlap for each variable: % overlap $= 100(1 - 0.5 \Sigma | P_{x,i} - P_{y,i}|)$ where $P_{x,i}$ and $P_{y,i}$ are the respective frequencies for males and females in each class for a given type of behavior. An overlap of 100% indicates that males and females acted identically in regard to the type of behavior examined, whereas 0% overlap indicates completely non-overlapping behavior.

RESULTS

There were 6,407 foraging observations of all seven groups ranging from a low of 794 in group 7 to a high of 1,152 in group 2. Observations of males ($n = 3,769$) ranged from 403 in group 7 to a high of 576 in group 6. Observations of females ($n = 2,638$) ranged from 269 (group 4) to 502 (group 2).

Method of Foraging.—Scaling was the most commonly used foraging method for males in all seven groups, ranging from 40 to 52% of the total observations ($n = 3,769$; Fig. 1), followed closely by probing. However, females in five of the seven groups used probing more commonly than scaling ($n = 2,638$; Fig. 1). Foraging method significantly differed between males and females for all groups combined, primarily because females tended to probe more ($F_{3,297} = 2.89$, $P = 0.04$).

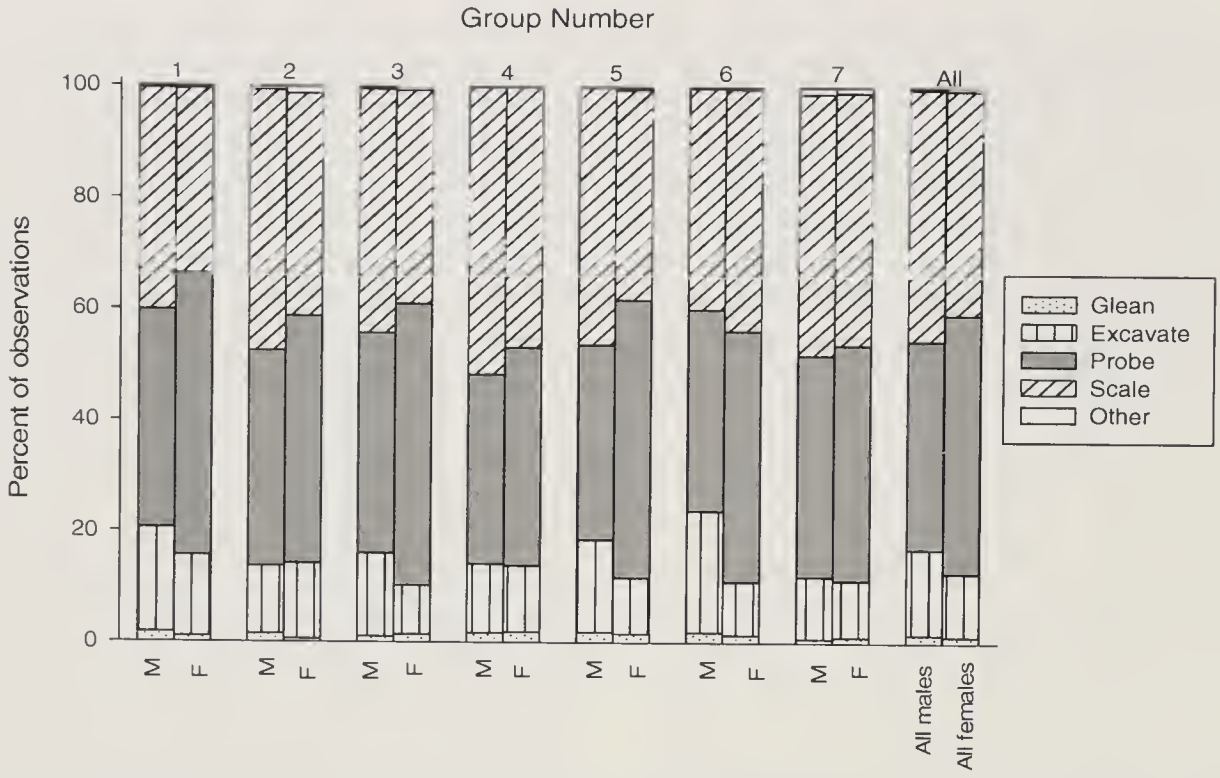

FIG. 1. Foraging method of male and female Red-cockaded Woodpeckers at the Savannah River Site, South Carolina, 1992–1995.

Substrate.—Males strongly preferred the trunk as the foraging substrate with 73 to 87% of observations occurring there (Fig. 2). For all groups combined, 79% of all male foraging was on the trunk surface, followed by 10% on a live limb, and 11% on a dead limb (Fig. 2). Females in each group had a stronger preference for foraging on the trunk than males and used that surface a minimum of 87% of the time (Fig. 2). Overall, 93% of all female foraging observations were on the trunk, followed by 4% on a live limb, and 2% on a dead limb. Occasionally males and females were observed foraging on cones (19 instances for males, 7 instances for females), and there was one instance of a female foraging on the ground. There was a significant difference in foraging substrate selection in every group and for all groups combined between males and females (all F values ≥ 3.79, all $P \leq 0.03$).

Tree Species Selection.—At least 98% of all foraging by males and females, regardless of group, occurred in pine trees. Overall for males there were 27 (0.7%) instances and up to 1% of observations for groups foraging in hardwood trees. Females were observed foraging in hardwoods on 20 instances (0.8%) and 2% of observations by group.

There was a decided preference by both males and females to forage in longleaf pines and this did not seem to be the result of tree dbh or age. The mean overall dbh values for pine species showed that, on average, longleaf pine trees available at SRS were 1.0 cm larger than loblolly pines and 2.8 cm larger than slash pine trees. Mean tree age of longleaf pine exceeded that of loblolly pine by 0.6 to 8.5 years but, in some groups, the mean age of the available loblolly pines exceeded that of longleaf by 0.3 to 5.0 years. For example, in group 1, loblolly pines on average were bigger (larger dbh) and older than longleaf pines. The latter species was most frequently used for foraging by males in all groups (range 69 to 90%) and accounted for 79% of all male observations ($n = 3,743$). Females also preferred to forage in longleaf pine trees, in which 78% of observations occurred (range 62–94% in the 7 groups). Loblolly and slash pine also were used, but to a much less extent. There was a significant difference in tree species selection by males and females in two of the seven groups (F values ≥ 4.60, P values < 0.02); however, considering all male and female observations combined, there was no significant difference in tree species selection ($F_{2,196} = 0.11$, $P = 0.91$).

Tree species selection by males differed from expected on the basis of tree species availability in all groups and for all males combined (all $F \geq 4.23$, all $P \leq 0.04$). Females in all but group 2 did not use tree species in the same proportion as available (all $F \geq 4.79$, all $P \leq 0.03$). Males in all

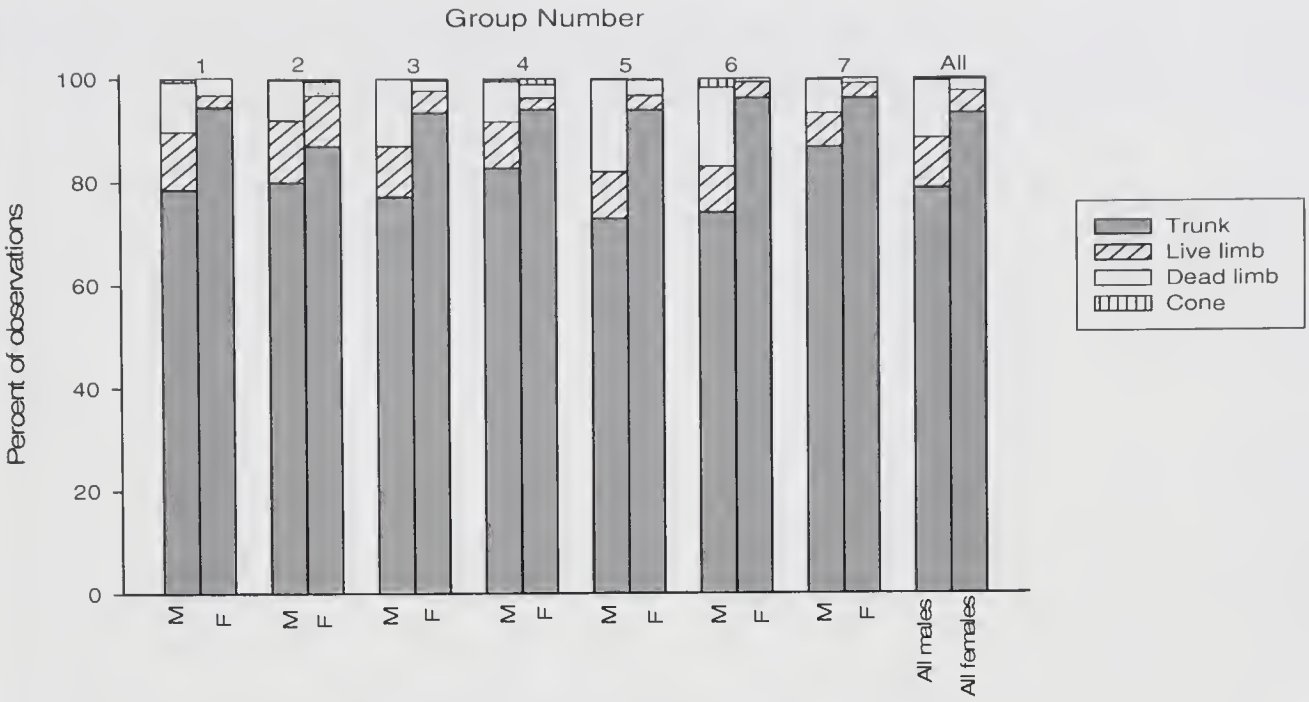

FIG. 2. Substrates used by foraging male and female Red-cockaded Woodpeckers at the Savannah River Site, South Carolina, 1992–1995.

groups and females in five of the seven groups foraged more in longleaf pines than expected based on availability.

Foraging Height.—Mean foraging height of males ranged from 9.5 ± 0.6 m in group 1 to 12.7 ± 0.4 m in group 5 (Table 1). Mean foraging height of females ranged from 7.5 ± 0.5 m in group 1 to 11.8 ± 0.4 m in group 5 (Table 1). Mean foraging height for males in two groups was higher than for females ($F \geq 6.0$, $P \leq 0.03$; Table 1). Foraging height for males for all groups combined was higher (11.1 ± 0.5 m) than for females (9.8 ± 0.5 m; $F_{1,6} = 17.67$, $P = 0.006$; Table 1).

Tree Height.—Mean heights of trees selected for foraging by males ranged from 17.6 ± 0.6 m in group 1 to 21.5 ± 0.3 m in group 5. Mean tree height selection by females ranged from 17.1 ± 0.6 to 21.3 ± 0.3 for groups 1 and 5, respectively. Mean tree height selection for all male observations combined (19.6 ± 0.5 m) was not different than for females (19.6 ± 0.5 m; $F_{1,6} = 0.02$, $P = 0.90$). There was no difference in mean tree heights between males and females in five of the seven groups (all $F \leq 0.42$, all $P \geq 0.53$) or between males and females within any group ($F \geq 4.49$, $P > 0.05$).

There was no difference for five of the groups comparing the distribution of observations for male versus female tree height selection (all $F \leq 1.39$, all $P \geq 0.24$). Nor was there a difference between males and females for all groups combined in distribution of observations by tree height ($F_{7,693} = 0.28$, $P = 0.96$).

Males and females in every group and for all groups combined did not randomly select trees by height (all $F \geq 10.56$, all $P \leq 0.001$). Both males and females avoided shorter trees (those less than 12 m), either avoided or used in proportion to availability mid-sized trees (12–18 m), and strongly preferred trees >18 m in height.

Tree Condition.—Both males and females heavily foraged on live trees (average of 90% of male and 91% of female foraging observations). There was no difference in selection of trees by condition (alive, dead, or dying) between males and females in five of the groups and for all groups combined ($F \leq 2.33$, $P \geq 0.12$). There was a difference between males and females in two groups ($F_{2,34} = 6.06$, $P = 0.006$; $F_{1,12} = 53.2$, $P < 0.0001$; groups 2 and 7, respectively) and males in both groups used dying trees more than females.

Diameter at Breast Height (dbh).—There was a difference in mean diameter at breast height of trees selected by males versus females for two of the seven groups. Females in group 6 ($F_{1,14} = 6.23$, $P = 0.03$) and group 7 ($F_{1,11} = 9.22$, $P = 0.01$) selected trees with larger dbh than males. Overall, there was no difference in mean dbh of trees selected for foraging by males and females in all groups combined ($F_{1,6} = 0.39$, $P = 0.55$).

TABLE 1. Foraging height (m) of male and female Red-cockaded Woodpeckers by seven groups and all groups combined at the Savannah River Site, South Carolina, 1992–1995.

	Percent observations							
	Group 1		Group 2		Group 3		Group 4	
Foraging height	M	F	M	F	M	F	M	F
<3	4.9	16.1	5.7	13.0	2.3	9.1	4.7	10.4
≥3–6	13.5	23.2	15.1	14.3	8.9	16.5	10.3	17.8
≥6–9	25.8	25.7	22.0	16.9	16.9	18.2	20.0	21.6
≥9–12	26.4	14.9	21.7	20.5	23.0	16.2	24.7	20.1
≥12–15	18.4	13.4	16.6	16.1	27.3	17.6	16.1	15.2
≥15–18	7.4	5.5	10.8	11.6	16.2	15.6	14.6	7.4
≥18–21	2.2	1.0	5.9	6.6	4.6	5.4	6.9	5.6
≥21–24	0.8	0.0	1.2	0.2	0.7	1.1	1.7	1.5
≥24	0.2	0.0	0.5	0.0	0.0	0.3	0.7	0.4
Ground or no data	0.4	0.3	0.6	0.8	0.0	0.0	0.3	0.0
Sample size	509	398	646	500	561	352	589	269
LSMeans ± SE	9.5 ± 0.6	7.5 ± 0.5	10.4 ± 0.3	9.8 ± 0.3	11.7 ± 0.7	9.0 ± 0.8	11.1 ± 0.5	9.6 ± 0.7
F value[a]	$F_{1,11} = 6.54$		$F_{1,16} = 1.67$		$F_{1,13} = 6.00$		$F_{1,14} = 3.00$	
	$P = 0.03$		$P = 0.21$		$P = 0.03$		$P = 0.10$	

	Group 5		Group 6		Group 7		All groups combined	
	M	F	M	F	M	F	M	F
	1.9	6.2	7.8	13.4	3.2	12.0	4.5	11.5
	3.4	8.5	14.8	22.6	9.2	14.3	11.0	16.3
	11.5	14.7	17.4	14.7	22.3	20.5	19.5	18.8
	23.9	23.9	22.7	20.6	26.1	20.0	23.9	19.5
	32.1	23.2	20.3	15.1	20.1	15.9	21.3	16.8
	18.5	15.6	10.8	9.6	10.7	9.2	12.7	10.9
	6.5	5.8	5.4	3.1	6.5	5.9	5.4	5.0
	1.1	0.5	0.4	1.0	1.7	2.3	1.1	0.7
	0.2	0.0	0.2	0.0	0.3	0.0	0.3	0.1
	1.1	1.6	0.4	0.0	0.0	0.0	0.4	0.4
	472	428	575	292	402	390	3,754	2,629
	12.7 ± 0.4	11.8 ± 0.4	10.5 ± 0.6	9.4 ± 0.8	11.9 ± 0.9	10.8 ± 0.84	11.1 ± 0.5	9.8 ± 0.5
	$F_{1,13} = 2.38$		$F_{1,14} = 1.22$		$F_{1,11} = 0.78$		$F_{1,6} = 17.67$	
	$P = 0.15$		$P = 0.28$		$P = 0.40$		$P = 0.006$	

[a] F and df values from Proc Mixed model; Note for df of x and y as given in $F_{x,y}$, x represents $k - 1$ and y is calculated by the clustering program.

There was a difference between males and females in two of the groups when comparing tree selection by distribution of observations by dbh size class with females using trees with larger dbh (group 6, $F_{7,105} = 3.78$, $P = 0.001$; and group 7, $F_{7,84} = 5.39$, $P < 0.0001$). There were no male/female differences in distribution of observations for dbh size class intervals in the other five groups and for all groups combined (all F values ≤ 1.31, $P \geq 0.26$).

Males and females did not randomly select trees on the basis of dbh (all $F \geq 9.68$, all $P \leq 0.001$). Both males and females avoided foraging in trees ≤20 cm dbh and displayed strong preferences for the moderate and larger dbh size classes.

Longleaf and loblolly pine trees were the two most common pine species in the habitat. The mean dbh for longleaf pine trees available to three groups was higher than for loblolly pine (Table 2); however, loblolly pine for two groups had higher mean dbh values (all $P < 0.001$). There was no difference in mean dbh values between longleaf and loblolly pine trees in the remaining two groups (Table 2). The available longleaf pines had a higher mean dbh (longleaf pine = 17.9 ± 0.2 cm vs. loblolly pine = 16.8 ± 0.2 cm, $P = 0.004$; Table 2) for all groups combined.

Tree Age.—Females in group 5 (mean = 39.9 ± 0.2 years vs. mean = 39.3 ± 0.2 years; $F_{1,13} = 5.27$, $P = 0.04$) foraged more on older trees than males (Table 3). There was no difference between

TABLE 2. Tree species availability (least-squares means ± SE) for tree age (yrs) and diameter at breast height (dbh) (cm) for foraging Red-cockaded Woodpeckers at the Savannah River Site, South Carolina, 1992–1995.

	Tree age					Tree dbh				
	Longleaf pine	Loblolly pine	Slash pine	Sand pine		Longleaf pine	Loblolly pine	Slash pine	Sand pine	
RCW group	Age sig. dif.[b]	Age sig. dif.[b]	Age sig. dif.[b]	Age sig. dif.[b]	*F*-value[a], *P*-value, sample size	dbh sig. dif.[b]	dbh sig. dif.[b]	dbh sig. dif.[b]	dbh sig. dif.[b]	*F*-value[a], *P*-value, sample size
1	23.6 ± 0.5^{A}	28.1 ± 1.0^{B}		41.3 ± 2.5^{C}	$F = 30.44$ $P < 0.0001$ $n = 806$	14.8 ± 0.4^{A}	19.3 ± 0.7^{B}		33.0 ± 2.0^{C}	$F = 51.98$ $P < 0.0001$ $n = 1,012$
2	24.8 ± 0.3^{A}	25.1 ± 0.9^{A}			$F = 0.07$ $P > 0.79$ $n = 1,603$	16.1 ± 0.2^{A}	15.1 ± 0.6^{A}			$F = 2.15$ $P = 0.14$ $n = 1,967$
3	27.6 ± 0.6^{A}	23.6 ± 0.5^{B}			$F = 29.96$ $P < 0.0001$ $n = 801$	22.1 ± 0.7^{A}	17.4 ± 0.4^{B}			$F = 36.46$ $P < 0.0001$ $n = 1,235$
4	30.7 ± 0.9^{A}	35.7 ± 1.0^{B}	28.7 ± 1.3^{A}		$F = 11.22$ $P < 0.0001$ $n = 505$	16.8 ± 0.7^{A}	24.4 ± 0.8^{B}	15.8 ± 1.0^{A}		$F = 32.38$ $P < 0.0001$ $n = 679$
5	27.3 ± 0.4^{A}	19.2 ± 0.3^{B}			$F = 241.71$ $P < 0.0001$ $n = 1,355$	23.8 ± 0.5^{A}	14.6 ± 0.3^{B}			$F = 269.51$ $P < 0.0001$ $n = 1,691$
6	32.6 ± 0.9^{A}	24.1 ± 1.4^{B}			$F = 25.17$ $P < 0.0001$ $n = 407$	20.8 ± 0.9^{A}	17.7 ± 1.3^{B}			$F = 4.18$ $P = 0.04$ $n = 568$
7	24.4 ± 0.8^{A}	23.8 ± 2.1^{A}	20.1 ± 1.6^{A}	20.0 ± 11.7^{A}	$F = 1.98$ $P > 0.12$ $n = 293$	16.7 ± 0.6^{A}	18.2 ± 1.6^{A}	13.3 ± 1.2^{A}	14.2 ± 10.2^{A}	$F = 2.64$ $P = 0.05$ $n = 378$
All groups	26.2 ± 0.2^{A}	23.3 ± 0.3^{BD}	25.7 ± 0.9^{AD}	40.5 ± 2.3^{C}	$F = 39.29$ $P < 0.0001$ $n = 5,770$	17.9 ± 0.2^{A}	16.8 ± 0.2^{B}	15.0 ± 0.8^{B}	32.3 ± 2.3^{C}	$F = 21.33$ $P < 0.0001$ $n = 7,530$

[a] *F*-value based on Proc GLM comparison of least-squares means with Bonferroni adjustment for multiple comparisons.
[b] Significant difference comparing means of individual tree species with Bonferroni adjustment; same letters indicate no significant difference.

TABLE 3. Male and female Red-cockaded Woodpecker selection of foraging trees by tree age (yrs) in relation to tree age availability on the Savannah River Site, South Carolina, 1992–1995.

	Observed vs. expected number of observations											
	Group 1			Group 2			Group 3			Group 4		
Tree age	M	F	Expected[a]	M	F	Expected[a]	M	F	Expected[a]	M	F	Expected[a]
1 to 10	0.0	0.0	4.6	0.0	0.0	1.6	3.6	2.5	7.0	0.0	0.0	2.4
11–20	0.0	0.0	38.9	0.0	0.0	28.9	0.0	0.0	21.6	0.0	0.0	20.3
21–30	0.0	0.0	33.3	0.0	0.0	56.1	0.0	0.0	39.4	0.0	0.0	29.6
31–40	15.5	22.2	11.1	36.9	36.9	7.5	22.6	23.6	24.9	14.9	15.5	22.0
41–50	14.7	15.0	6.7	0.2	0.0	2.6	31.9	30.1	4.0	13.7	15.9	20.1
51–60	1.3	1.7	3.2	0.9	0.0	1.9	7.3	7.4	0.9	71.1	68.3	3.9
61–70	38.6	41.0	1.7	62.0	62.4	1.1	1.3	1.2	1.5	0.3	0.4	0.8
71–80	29.6	20.0	0.3	0.0	0.7	0.4	0.0	0.0	0.7	0.0	0.0	0.8
81–90	0.0	0.0	0.0	0.0	0.0	0.0	33.5	35.3	0.1	0.0	0.0	0.0
>90	0.4	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Sample size	477	361	809[b]	531	271	1,879	562	326	881[b]	592	265	592[b]
LSMeans ± SE	59.0 ± 1.2	55.8 ± 1.2		52.3 ± 2.4	55.0 ± 2.3		57.2 ± 1.3	57.8 ± 1.6		50.8 ± 1.2	50.2 ± 1.5	
Compare means[c]	$F_{1,8} = 3.54$ $P = 0.10$			$F_{1,14} = 0.66$ $P = 0.42$			$F_{1,12} = 0.09$ $P = 0.76$			$F_{1,14} = 0.09$ $P = 0.76$		
LR test[d] male vs. female	$F_{5,45} = 1.79$ $P = 0.13$			$F_{2,30} = 0.01$ $P = 0.99$			$F_{5,65} = 0.36$ $P = 0.88$			$F_{3,45} = 0.08$, $P = 0.97$		
LR test[d] actual vs. expected use	male: $F_{4,12} = 18.49$ $P < 0.0001$ female: $F_{4,20} = 14.51$ $P < 0.0001$			male: $F_{2,12} = 16.84$ $P = 0.0003$ female: $F_{2,16} = 7.76$ $P = 0.004$			male: $F_{4,28} = 47.36$ $P < 0.0001$ female: $F_{4,20} = 20.83$ $P < 0.0001$			male: $F_{3,27} = 30.36$ $P < 0.0001$ female: $F_{3,15} = 8.03$ $P = 0.002$		

	Group 5			Group 6			Group 7			All groups combined		
	0.0	0.0	8.8	15.3	10.1	1.4	0.0	0.0	6.8	2.7	1.7	4.3
	0.0	0.3	35.7	2.4	1.3	29.9	0.0	0.0	33.5	0.3	0.2	25.1
	0.0	0.3	35.7	2.4	1.3	29.9	0.0	0.0	33.5	0.3	0.2	25.1
	0.0	0.0	33.8	8.8	5.9	37.2	0.0	0.0	43.7	6.8	0.8	48.8
	84.1	76.1	18.3	15.3	24.8	16.3	24.7	20.7	8.5	24.3	32.9	13.7
	15.6	23.2	2.7	36.6	30.7	6.4	10.2	11.7	2.7	17.8	18.4	4.7
	0.0	0.0	0.3	21.1	26.1	2.9	62.6	65.2	3.1	23.3	23.2	1.7
	0.2	0.5	0.2	0.0	0.0	2.4	0.0	0.0	0.7	14.8	14.0	1.0
	0.0	0.0	0.2	0.6	1.0	3.0	0.0	0.0	1.0	4.1	3.3	0.6

TABLE 3. Continued.

	Group 5			Group 6			Group 7			All groups combined		
	0.0	0.0	0.1	0.0	0.0	0.5	0.0	0.0	0.0	5.3	5.0	0.1
	0.0	0.0	0.0	0.0	0.0	0.0	2.5	2.4	0.0	0.5	0.4	0.0
LSMeans ± SE	39.3 ± 0.2	39.9 ± 0.2		37.8 ± 1.2	41.7 ± 1.6		49.1 ± 1.1	48.8 ± 1.0		49.5 ± 2.9	49.9 ± 2.9	
Compare means[c]		$F_{1,13} = 5.3$			$F_{1,12} = 3.9$			$F_{1,8} = 0.03$			$F_{1,6} = 0.27$	
		$P =$			$P =$			$P = 0.86$			$P = 0.62$	
	0.04			0.07								
LR test[d] male vs. female	$F_{2,28} = 4.3, P = 0.02$			$F_{4,52} = 4.3, P = 0.005$			$F_{3,27} = 0.5, P = 0.66$			$F_{6,528} = 0.08, P = 0.99$		
LR test[d] actual vs. expected use	male: $F_{2,10} = 177.1, P < 0.0001$			male: $F_{2,18} = 90.9, P < 0.0001$			male: $F_{2,12} = 1185.00, P < 0.0001$			male: $F_{8,352} = 4.8, P < 0.0001$		
	female: $F_{2,16} = 248.8, P < 0.0001$			female: $F_{2,6} = 343.4, P < 0.0001$			female: $F_{2,6} = 50.0, P = 0.0002$			female: $F_{8,296} = 4.3, P < 0.0001$		

[a] Expected use based on the percent of trees of that age class.
[b] Number of trees measured.
[c] Means of males and females compared with *F*-test in Proc Mixed.
[d] LR = Rao-Scott modified likelihood ratio test in Proc SurveyFreq comparing distribution of observations to availability; df values denoted as $F_{x,y}$ where *x* represents the number of categories (i.e., age class intervals compared) and *y* is a reflection of the number of clusters in the test.

males and females for six of the seven groups and for all groups combined in tree age classes (all $F \leq 1.79$, all $P \geq 0.13$, Table 3). Neither males nor females randomly selected trees by age class (all $F \geq 4.25$, all $P \leq 0.002$). Both males and females used younger trees (<30 years of age) less than expected and preferred trees ≥30 years of age (Table 3).

Mean age was higher for longleaf pine than loblolly pine in three groups ($P < 0.0001$) within the 800-m radius circles centered on the nest tree of each group with the reverse true in two groups ($P < 0.0001$; Table 2). There was no difference in mean age between available longleaf and loblolly pines in groups 2 and 7 (Table 2). Mean tree age of longleaf pine (26.2 ± 0.2 years) was higher compared to loblolly pine (23.3 ± 0.3 years, $P < 0.0001$; Table 2) combining the 800-m circles of all groups.

Niche Breadth and Overlap.—Foraging variables that had the narrowest niche breadth were the same for males and females: tree species selection (1.54 vs. 1.57), tree condition (1.24 vs. 1.20), and substrate (1.56 vs. 1.15). Both males and females were most generalized in tree dbh (6.25 vs. 6.54), foraging height (5.78 vs. 6.41), tree height (4.85 vs. 4.91), and tree age (5.55 vs. 4.55). Niche overlap between males and females was ≥90% for foraging method (90.8%), tree species (99.0%), dbh (95.7%), tree height (96.4%), tree condition (98.3%), and tree age (90.9%). The least overlap between males and females was for substrate (85.6%) and foraging height (87.8%).

DISCUSSION

Results of foraging ecology studies of male and female Red-cockaded Woodpeckers in regard to foraging method have not been consistent (Ramey 1980, Hooper and Lennartz 1981, Rudolph et al. 2007). In my study, males scaled more than females in two groups, whereas females engaged more in probing. Red-cockaded Woodpeckers at SRS did not forage by excavating to the same extent observed at other locations, all of which had more mature pine habitat. It may be that young stands at SRS did not provide the deep, furrowed bark of older trees that would encourage more excavation. Culmen length is significantly longer in males than females (Mengel and Jackson 1977), which may contribute to the differences that have been observed. However, the Red-cockaded Woodpecker is one of the least sexually

dimorphic species of *Picoides* and, although difference in beak size could be an adaptation for differential foraging behavior, culmen length would seem to be insufficient to obviate the need to have other means to reduce intraspecific competition.

It has been reported that both males and females forage mostly on the trunk (Ligon 1968, Skorupa 1979, Ramey 1980, Hooper and Lennartz 1981). My results showed that males spent more time foraging on limbs than females, whereas females more frequently foraged on trunks. Ramey (1980) found variation in foraging site was the main difference between males and females, and there was substantial foraging in hardwoods, particularly by males. Pizzoni-Ardemani (1990) reported that male Red-cockaded Woodpeckers have longer beaks, toes, and legs, and shorter tails than females, which may be advantageous when clinging to branches and twigs on limbs. The shorter legs and longer tail of females may be beneficial when foraging on trunks (Pizzonni-Ardemani 1990), the common female foraging substrate.

Red-cockaded Woodpeckers forage on living pine trees and rarely use non-pine substrates (Ligon 1968, Hooper and Lennartz 1981, DeLotelle et al. 1983, Porter and Labisky 1986); however, DeLotelle et al. (1983) also found that 10% of foraging occurred in pond cypress *(Taxodium ascendens)* stands. Both males and females at SRS heavily used pine trees and at least 98% of all observations occurred there, similar to that reported by other studies (Ramey 1980; Zwicker and Walters 1999; Walters et al. 2000, 2002; Rudolph et al. 2007). I detected no difference between males and females in four of the groups and in all groups combined in use of different pine species. However, based on availability, both males (all groups) and females (5 of 7 groups) foraged in longleaf pine trees more than expected. Previous work on tree species selection produced conflicting results as to whether Red-cockaded Woodpeckers prefer a particular pine species (Nesbitt et al. 1978, Porter and Labisky 1986). Tree species selection can be confounded by tree age and size, presence of a hardwood midstory, and density of trees in the area.

All studies that examined foraging height of Red-cockaded Woodpeckers have reported that males forage higher in trees than females (Hooper and Lennartz 1981, Engstrom and Sanders 1997, Rudolph et al. 2007). However, in my study this was true of only two of the seven groups and all groups combined. It may not have been apparent that for most of the groups there was no difference in foraging height for males and females if only combined data had been analyzed. Habitat partitioning by foraging height could reduce competition for prey and permit specialization by gender so that trees are used more efficiently. Males are dominant to females and may be using the most productive portions of the foraging substrate.

Porter and Labisky (1986) reported that when Red-cockaded Woodpeckers foraged in stands that were usually avoided, they selected trees of greatest height and dbh. Ramey (1980) detected no significant difference in tree heights used by males and females. I also found there was little difference in tree height selection between males and females. Both strongly preferred taller and avoided shorter trees, probably reflecting the larger, more deeply fissured bark surface area of the taller trees.

Dying and recently dead pine trees, especially those with southern pine beetle (*Dendroctonus frontalis*), are an important foraging resource for Red-cockaded Woodpeckers, but the reported response by males/females has not been consistent. Hooper and Lennartz (1981), Repasky (1984), and this study found that male and female foraging was similar. Five of the groups and all groups combined in my study had no difference in foraging selection between males and females based on tree condition. Skorupa and MacFarlane (1976), Skorupa (1979), and Repasky (1984) reported that males foraged more frequently than females on dead and dying trees. The differences in the response may reflect the level and occurrence of insect infestations.

Hooper and Lennartz (1981) reported niche overlap between males and females was highest for tree condition (99%) and dbh (97%). Most overlap in my study occurred in tree species (99.0%) and tree condition (98.3%). Foraging height overlap was low (56%) in the study by Hooper and Lennartz (1981), but was 87.8% in my study. Higher niche overlap for foraging height and also similarity in foraging height for five of the seven groups in my study reflected the considerably younger forest than that studied by Hooper and Lennartz (1981) where there was less opportunity for vertical divergence in foraging height between males and females.

Hanula et al. (2000) sampled 300 living pine trees at SRS during the same time frame in which my study was conducted and found that arthropod biomass/tree increased with increasing stand age up to ~65–70 years, but the arthropod biomass/ha was highest in the youngest stands. Abundance and biomass of arthropods on each tree trunk was positively correlated with bark thickness and tree diameter, and negatively correlated with basal area (m^2/ha). There was no correlation of diversity, abundance, or biomass with arthropods on the tree trunk with site index, numbers of herbaceous plant genera in the understory, number of herbaceous plant stems, or percent ground cover by herbs. The characteristics of the stands, including average bark thickness and dbh, associated with greater arthropod abundance and biomass on the bark are positively correlated with tree age, but are subject to change depending on how stands are managed (Hanula et al. 2000). Current management guidelines at SRS include prescribed burning at least 2–3 times/10 years in active Red-cockaded Woodpecker clusters, midstory tree/shrub removal, thinning of overstory pines, suppression of pine beetle infestations, and extensive recommendations for regeneration (Edwards et al. 2000).

Hooper and Lennartz (1981) and Zwicker and Walters (1999) reported Red-cockaded Woodpeckers preferentially selected the largest trees with respect to dbh with no differences between males and females. My results were similar for five of the groups and for all groups combined. Both males and females consistently selected larger dbh trees based on availability, far more than expected on the basis of their presence in the habitat. Larger trees have more arboreal surface area available in which to forage per visit and probably richer resource patches/unit area than smaller trees.

All researchers who have investigated individual tree selection have found that large old trees are preferred over smaller, younger ones (DeLotelle et al. 1987, Jones and Hunt 1996, Hardesty et al. 1997, Walters et al. 2002). Age and size of pine trees are highly correlated until about age 80 (Platt et al. 1988). It is not clear whether tree size (dbh), age, or both is the more important determinant of tree selection by foraging Red-cockaded Woodpeckers. There was a significant difference between males and females in my study in mean tree age selected in four of the groups and in all groups combined; however, it was not always the same gender that had the stronger selection for older trees. Females tended to select trees with higher dbh values. Females spend more time foraging on the trunks than males, and it is likely this difference reflects females taking advantage of the additional foraging surface area provided on larger trees. Both males and females avoided foraging in trees <30 years of age with some groups not using them. There was a strong preference by both males and females to use trees at least 60 years of age in my study. Males and females still preferred to forage on older trees even though a majority of stands at SRS were considered young.

There was little difference in dbh size among the pines at the SRS, but longleaf pines on average were strongly preferred as foraging substrate by both males and females. Loblolly, the second most commonly available pine species within the home ranges next to longleaf pine, tended to be selected against. The mean age of longleaf pine in some groups exceeds that of loblolly pine, but in other groups the opposite is true. Males (69.4% of observations) and females (72.7% of observations) strongly selected longleaf pine trees in relation to the predicted use of longleaf pine (46.2%). Red-cockaded Woodpeckers evolved in a mixed-age forest containing only a relatively small proportion of young pine trees (Frost 1993) and in a landscape dominated by longleaf pine; thus, they may be more adapted to foraging on surfaces of old, large pine trees. It is logical to assume they are best equipped morphologically and behaviorally to use longleaf pine. The strong preference by both males and females to use longleaf pine does not appear to be strictly the result of tree size or age.

Habitat segregation observed in foraging Red-cockaded Woodpeckers may be designed to reduce competition between males and females to allow more efficient use of the available foraging habitat. The more socially dominant males may cause females to use less productive areas. It is plausible that partitioning by gender in this species may be an efficient mechanism to facilitate cohesion of the group by reducing male/female competition and aggression. Breeding males at SRS tended to hold their territories until they disappeared (and were presumed dead). Females were more flexible in maintaining their pair bonds. Thus, it would be beneficial to the group to minimize aggressive encounters and to maximize social cohesion of group members. This

may be the mechanism that developed differences between males and females as documented at this younger growth site and elsewhere.

Red-cockaded Woodpecker mean reproductive success (fledglings/pair) at SRS ranged from 1.4 to 3.4 with the highest rates (2.8–3.4) observed for groups with at least 10,000 pine stems ≥25.4 cm dbh within 800 m of the nest cavity (Franzreb 2004). Reproductive success was significantly related to number of available pine stems ≥25.4 cm dbh (Franzreb 2004). Typical mean reproductive rates in other parts of the range were 1.34–1.67 fledglings/pair (Conner et al. 2001). Higher rates at SRS, rather than due mainly to habitat quality, are possibly the result of the unusually intensive management of the species on the site, including installation of artificial cavity inserts, removal of cavity competitors, translocating birds to re-establish a pair where one member has been lost, frequent monitoring of cavities to detect damage to artificial inserts, and frequent monitoring of all individuals in the population (Franzreb 2004).

Subsequent to initiation of these management activities, the population level has increased to ~196 adults and fledglings in 2006 (John Blake, pers. comm.) from a low of four birds in 1986 (Franzreb 1997). Development of the technique to install artificial cavity inserts for the Red-cockaded Woodpecker was pioneered at SRS (Allen 1991) and installation of these devices has been a widely used management tool in many parts of the range. Artificial inserts at SRS were used by 47% of the birds in comparison to 53% that used naturally excavated cavities for the nest location during my study (K. E. Franzreb, unpubl. data). It is likely that Red-cockaded Woodpeckers would not have persisted at SRS without the assistance provided by these management actions.

Current federal guidelines for managing Red-cockaded Woodpecker foraging habitat are complex and address factors including type of forest regeneration, rotation age, basal area, and home-range size needed per group (USFWS 2003). Management and recovery of the Red-cockaded Woodpecker have focused on providing suitable foraging habitat in more mature and older pine stands than typically found at SRS. The results of my study indicate that younger forest stands, as long as they are at least 30 years of age, may provide acceptable foraging habitat and should not automatically be regarded as unacceptable or sub-optimal.

Younger trees (preferably at least 40 cm dbh) in which managers have either installed artificial cavity inserts or drilled cavities are necessary to provide for nesting and night roosting if older trees are insufficient for natural cavity excavation. It is preferable to provide trees of sufficient size so birds can create their own cavities rather than rely on artificial inserts. Allowing pines to age to ≥60 years, preferably even older, provides better foraging habitat and trees of sufficient size for birds to excavate their own cavities. Maintaining the site in just young pines will not maintain a self-sustaining population without continued intensive management actions as there will be insufficient trees for natural cavity excavation nor would there be the larger trees that are preferred for foraging. The need to provide larger, older pines has been recognized in the SRS management plan for the Red-cockaded Woodpecker, which calls for a number of proactive actions including a rotation age of 120 and 100 years for longleaf pine and loblolly pine stands, respectively, in the main Red-cockaded Woodpecker management area (Edwards et al. 2000). Older pines will be optimal foraging substrate for both male and female Red-cockaded Woodpeckers and will provide the large trees needed for natural cavity excavation.

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FORAGING HABITS AND HABITAT USE BY EDIBLE-NEST AND GLOSSY SWIFTLETS IN THE ANDAMAN ISLANDS, INDIA

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ABSTRACT.—Foraging habits and habitats of exclusive aerial insectivores, the Edible-nest Swiftlet (*Aerodramus fuciphagus inexpectatus*) and Glossy Swiftlet (*Collocalia esculenta affinis*), were studied in Andaman Islands, India. Observations were made during January to June 2004 between 0500 and 1800 hrs at four locations in the forest and on open paddy land. Edible-nest and Glossy swiftlets, respectively, spent ($\bar{x} \pm$ SD) 17.2 ± 11.4% and 25.8 ± 15.6% of their time foraging with significant temporal variations. Glossy Swiftlets had spatial variations in twist, flutter, and tail-wing-open foraging maneuvers. This species also had diurnal variations in flock size, which were positively correlated with feeding attempts. Both swiftlets shared all microhabitats except Inside Forest Canopy and Inside Stream Bank Canopy. Microhabitat use did not vary significantly in Below Stream Bank Canopy, >10 m Above Forest Canopy, >30 m Above Ground, and Above Forest Canopy for Edible-nest Swiftlets. Inside Forest Canopy and Inside Stream Bank Canopy categories for Glossy Swiftlets were relatively important in descending order. Deforestation near and distant from caves used by swiftlets for breeding in the islands can severely affect the wild population of both species. *Received 2 September 2009. Accepted 11 January 2010.*

Swiftlets (Apodidae) are exclusively aerial insectivores and land only on their nesting and roosting sites in caves or cave-like conditions (Medway 1962, Charles 1987, Chantler and Driessens 2000, Nguyen et al. 2002). Swiftlets have wings well adapted for long and fast flights (Norberg 1986, Chantler 1999). However, a single observation of a Glossy Swiftlet (*Collocalia esculenta*) perching on a tree was reported by Spennemann (1928). Detailed information about aerial and foraging habits, and habitat and microhabitat requirements of most swiftlet species is scarce. Swiftlets have large foraging ranges and travel far from caves used for breeding. Medway (1962) observed *Aerodramus maximus* and *A. salanganus* flying >24 km from their breeding caves. Swiftlet abundance has been mostly studied in different habitats or air spaces whereas their behaviors have been briefly studied (Medway 1962, Harrison 1972, Hails and Amirrudin 1981, Waugh and Hails 1983, Tarburton 1986, Charles 1987, Lim and Cranbrook 2002, Nguyen et al. 2002). Most studies have recorded the occurrences of swiftlet species in different habitats and altitudes in relation to breeding seasonality, and weather conditions with information on diet and general foraging habits (Medway 1962, Harrison 1972, Langham 1980, Hails and Amirrudin 1981, Nguyen 1983, Waugh and Hails 1983, Laurie and Tompkins 2000, Lim and Cranbrook 2002, Nguyen et al. 2002). The breeding biology and breeding habitats of the economically valuable Edible-nest Swiftlet (*A. fuciphagus*) are well documented in different parts of their ranges (Lim and Cranbrook 2002, Nguyen et al. 2002).

India has four species of swiftlets; Indian Swiftlet (*A. unicolor*), Himalayan Swiftlet (*A. brevirostris*), Edible-nest Swiftlet, and Glossy Swiftlet. The later two species are distributed in the Andaman and Nicobar Islands. The Edible-nest Swiftlet (*A. fuciphagus inexpectatus*), endemic to the Andaman and Nicobar Islands, is known to build highly commercial white edible nests exclusively made up of its saliva (Medway 1963, Lau and Melville 1994, Chantler 1999) inside limestone caves throughout the island arc. The Glossy Swiftlet (*C. esculenta affinis*), also endemic to the Andaman and Nicobar Islands, commonly constructs its nest using saliva as the cementing material to bind nesting materials including mosses, leaves, flowers, and *Casuarina* needles inside caves, suitable houses and buildings, under jetties, etc. (Medway 1963, Chantler 1999). Uncontrolled exploitation of nests caused a decline of ~80% in the Edible-nest Swiftlet population between 1990 and 2000 (Sankaran 2001). *In-situ* and the *ex-situ* conservation programs for the species were initiated at selected sites to arrest this population decline in the Andaman and Nicobar Islands. The *in-situ* population of the Edible-nest Swiftlet is being protected during the breeding season. The ability to breed in diverse habitats made the Glossy Swiftlet an important part of the *ex-situ* conser-

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vation program for fostering the Edible-nest Swiftlet (Sankaran and Manchi 2008).

The Edible-nest Swiftlet and Glossy Swiftlet of the Andaman and Nicobar Islands have not been studied extensively except for status surveys and brief information on their breeding seasonality (Sankaran 1995, 1998, 2001). Our objectives were to study: (1) aerial and foraging habits, (2) spatial and temporal variations in foraging habits, and (3) habitats with the microhabitat requirements of both species near their breeding sites.

METHODS

Study Area.—Andaman and Nicobar Islands in the northeastern Indian Ocean are the peaks of a submerged continuous mountain ridge arching from Arakan Yoma in the north to Sumatra in the south, between 06° 45′ N and 13° 41′ N, and 92° 12′ E and 93° 57′ E (Manchi and Sankaran 2009). Data were collected near the breeding sites of Edible-nest and Glossy swiftlets at Chalis-ek (a single hillock with a group of inland limestone caves) and Pattilevel (human habitation area adjacent to the Chalis-ek hillock) near Ramnagar, in the southeastern part of North Andaman Island. The Chalis-ek cave complex had 650 breeding pairs of Edible-nest Swiftlets. Five caves were used by 117 breeding pairs of the Glossy Swiftlet, along with pairs of Edible-nest Swiftlets. Chota tikree, another small hillock within 0.5 km of Chalis-ek, had 16 breeding pairs of Edible-nest Swiftlets and seven breeding pairs of Glossy Swiftlets in four caves. The Chalis-ek and Pattilevel areas have evergreen, semi-evergreen, and dry deciduous habitats (Sankaran 1998). People inhabiting the area altered part of the forested land into paddy fields. There are two major open paddy fields (within 1–2 km of the Chalis-ek hillock. The remaining forest in the area is under immense pressure of deforestation.

Data Collection.—Scan sampling (Altmann 1974) was used to record foraging behavior of Edible-nest and Glossy swiftlets between 0500 and 1800 hrs (Indian Standard Time). Observations were made at four points every 2 weeks from January to June 2004. Ten-minute observations were made every 15 min. The number of birds was recorded after each observation. There were 2,086 observations in 624 hrs for both species. Activity performed, habitat, microhabitat type, and flock size were recorded for each encounter. We developed terminology for describing the aerial behavior of swiftlets.

Fly/glide.—The flight with wing beats was recorded as 'fly' and flight without wing beat was recorded as 'glide.' These two flying patterns are combined as *Fly/glide.*

Feeding Attempts (Foraging Maneuvers).—Observations were limited to recording feeding attempts by presuming that different behaviors/activities were performed to capture different kinds of prey. Five types of behaviors were recorded as *Foraging Maneuvers.*

Twist.—The bird makes a sudden twist while gliding.

Fly-pause.—A fast-flying individual occasionally makes a sudden pause for a second and then moves on with a slight twist.

Roll.—The individual catches prey in its beak and rolls down. Birds were observed rolling down for about 2 sec.

Flutter.—A hover performed with a rapid wing beat and a pause in flight.

Tail and wing open.—A pre-planned position to capture prey once observed. Wing and tail feathers are stretched while approaching the prey and a small twist or flutter is performed during capture. This event takes at most 2 sec.

Call.—There are two types of calls: tik-tik-tik and chirk-chirk-chirk made in flight.

Follow.—Individuals were observed chasing each other in flight.

Preen.—Preening during flight.

Defecate.—Defecating during flight.

Carry Nest Material.—Swiftlets collect and carry nest materials in flight.

Major studies related to food preferences (Harrison 1972, Hails and Amirrudin 1981, Laurie and Tompkins 2000, Nguyen et al. 2002) were based on gut content and bolus collection; these were not attempted in our study to avoid sacrifice of any individual. We presumed that gut content and bolus collection during feeding visits by adults would adversely affect nesting success.

The Point-centered Quarter Method (Mitchell 2001) was used to study tree diversity in the forests of Chalis-ek. Habitats were classified following Hails and Amirrudin (1981) with separation of habitats into microhabitats dependent on foraging heights in air space. Heights considered for segregating microhabitats differed from those of Hails and Amirrudin (1981) per the suitability of the study area based on canopy levels. Forest habitat was categorized into four microhabitats: (1) Below Forest Canopy, (2) Inside Forest Canopy, (3) 0–10 m Above Forest

TABLE 1. Activity budgets ($\bar{x} \pm$ SD, %) of Edible-nest and Glossy swiftlets near breeding caves at Chalis-ek, North Andaman Island, India.

Activity	Edible-nest Swiftlet n = 719	Glossy Swiftlet n = 1,265	Mann-Whitney test	
			Z	P
Fly/glide	74.42 ± 16.10	84.60 ± 17.50	−13.609	<0.001
Feeding attempts	14.03 ± 12.30	13.75 ± 17.20	−5.217	<0.001
Call	2.08 ± 5.10	0.67 ± 3.30	−14.572	<0.001
Follow	9.47 ± 12.10	0.98 ± 4.20	−25.020	<0.001

Canopy, and (4) >10 m Above Forest Canopy. The open paddy lands developed through deforestation had streams with vegetation along the stream banks. This vegetation was included in the open land habitat which was divided into six microhabitats: (1) 0–5 m Above Ground, (2) 5–30 m Above Ground, (3) >30 m Above Ground, (4) Below Stream Bank Canopy, (5) Inside Stream Bank Canopy, and (6) 0–10 m Above Stream Bank Canopy. Temperature was recorded using a Zeal thermometer. A rain gauge was placed at the top of the hill in an open canopy area to record the amount of rainfall.

Statistical Analyses.—Percentage of time spent on each activity was estimated in each set of observations from instantaneous scan samples and the proportion of time spent on different aerial activities was calculated. Behaviors including preening, defecating, and carrying nest material were collectively performed <0.1% of the time by both species, and were not included in the statistical analyses. Variations in activities of Edible-nest and Glossy swiftlets were calculated with Mann-Whitney *U*-tests (*Z*). Days were divided into four sets of time: 0500–0815 hrs (early morning), 0815–1130 hrs (late morning), 1130–1445 hrs (afternoon), and 1445–1800 hrs (late afternoon). The data were arcsine transformed for one-way ANOVAs. Kruskal-Wallis tests and one-way ANOVAs were performed to examine temporal and spatial variations in activities overall, different behaviors separately, and activities performed in different microhabitats. Identification of the differing means was achieved by a Tukey's test for the detailed activity patterns when significant differences were found. All statistical analyses were also conducted with the data on feeding attempts to derive or understand foraging maneuvering patterns. Pearson's correlation test (r) was performed to examine the relation between foraging frequency and foraging flock size. Diurnal variation in size of the foraging flock was also described. An Important Value Index (IVI) of trees was calculated following Mitchell (2001). Chi-square tests (Crosstab: contingency table) were used to confirm distinctness of the species in terms of microhabitat use. Binary logistic regression analysis was performed to estimate use and relative importance of each microhabitat. All statistical tests were performed using Microsoft Excel 2003 and SPSS software, Version 10.0 (SPSS Institute 1998).

RESULTS

Edible-nest Swiftlets were encountered 41,959 times in 719 observations with an average ($\bar{x} \pm$ SD) of 58.4 ± 41.6 activities per set. There were 36,906 encounters of Glossy Swiftlets in 1,265 sets of observations with an average of 29.2 ± 36.5 activities per 10-min period.

Aerial Activity Budget.—Edible-nest and Glossy swiftlets in flight performed fly/glide, feeding attempts, follow, and call in descending order of their frequencies of occurrence. Preen, defecate, and nest material transport were collectively performed for 0.07% of the total activities and were not included in further analyses. The proportions of time by the two species for different activities varied significantly (Table 1).

Spatio-temporal Variation in Aerial Activity.—Edible-nest and Glossy swiftlets had significant temporal and spatial variations in their overall active periods (Fig. 1). The monthly active period varied ($\chi^2 = 105$, $P < 0.001$) for Edible-nest and Glossy swiftlets ($\chi^2 = 23$, $P < 0.001$). The diurnal active period varied for Edible-nest ($\chi^2 = 55.896$, $P < 0.001$) and Glossy swiftlets ($\chi^2 = 8.464$, $P = 0.037$). Spatial variation in active period was also shown by Edible-nest ($\chi^2 = 58.081$, $P < 0.001$) and Glossy swiftlets ($\chi^2 = 293.654$, $P < 0.001$). Individual aerial activities of both species, except feeding attempts for Edible-nest Swiftlets, had significant monthly

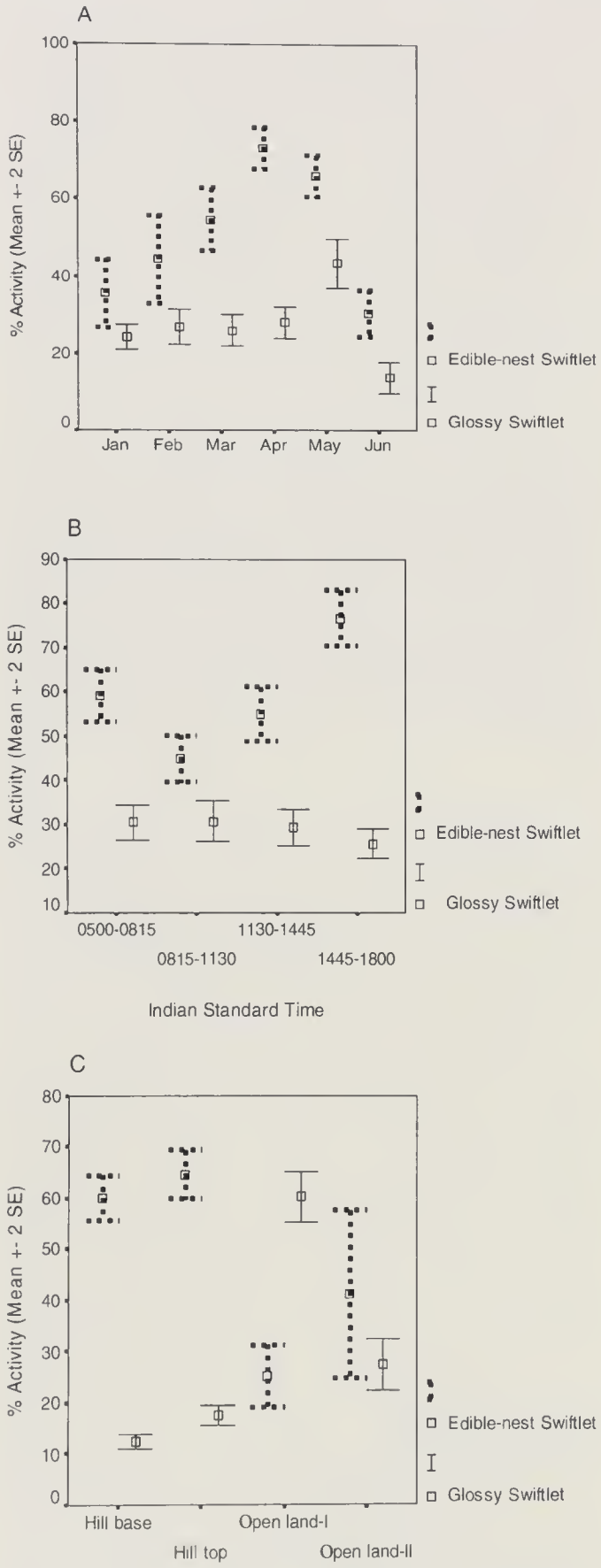

FIG. 1. Spatio-temporal variation (A = monthly, B = diurnal, and C = location; %) in activities of Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Island, India.

variations (Table 2). All activities had significant diurnal variations except feeding attempts for both species, and call behavior for the Edible-nest Swiftlet (Table 3). All the other activities, unlike fly/glide and call, had significant spatial variations (Table 4).

Foraging Activity Budget.—Edible-nest and Glossy swiftlets spent ($\bar{x} \pm$ SD) 17.2 ± 11.4 and 25.8 ± 15.6% of their time in feeding attempts, respectively. Both species spent substantial time on twist, flutter, tail-wing-open, fly-pause, and roll in descending order. The proportion of time spent on different foraging maneuvers varied significantly (Table 5).

Spatio-temporal Variations in Foraging Activities.—Both species had significant spatial (Edible-nest Swiftlet: $\chi^2 = 61.236$, $P < 0.001$; Glossy Swiftlet: $\chi^2 = 84.702$, $P < 0.001$) and monthly (Edible-nest Swiftlet: $\chi^2 = 19.588$, $P < 0.001$; Glossy Swiftlet: $\chi^2 = 53.952$, $P < 0.001$) variations in time spent in feeding attempts. However, significant temporal variations across the day were not apparent (Fig. 2). Foraging maneuvers, except flutter by Edible-nest Swiftlets and roll by Glossy Swiftlets, had significant monthly variations (Table 6), but roll had significant diurnal variations by Glossy Swiftlets (Table 7). Twist alone in both species, and tail-wing-open in Glossy Swiftlets, had significant spatial variations (Table 8).

Foraging Flock Size.—Edible-nest Swiftlets foraged in significantly larger flocks ($\bar{x} \pm$ SD, 9.4 ± 3.5 individuals; min = 3, max = 17) before returning to roosting caves between 1700 and 1800 hrs ($\chi^2 = 120.944$, $P < 0.001$). Glossy Swiftlets also formed comparatively large flocks ($\bar{x} \pm$ SD, 5.7 ± 2.4 individuals; min = 2, max = 11) between 1700 and 1800 hrs without any significant diurnal variation (Fig. 3). Edible-nest and Glossy swiftlets had significant correlations ($r = 0.400$, $P < 0.001$ and $r = 0.307$, $P < 0.001$, respectively), between foraging flock size and frequency of feeding attempts. This correlation did not change when partial correlation was performed by controlling for month, location, and hours (Edible-nest Swiftlet: $r = 0.420$, $P < 0.001$, Glossy Swiftlet: $r = 0.370$, $P < 0.001$).

Quantification of Vegetation.—Chalis-ek had 63 species of trees in the area. The forest community was dominated by *Pterocarpus dalbergioides* (IVI = 35.7) followed by *Diospyros crumenata* (IVI = 22.4) and *Drypetes andamanica* (IVI = 21.3).

Habitats and Microhabitats.—Foraging individuals of both species were encountered significantly more in forest than open land (Edible-nest Swiftlet: $\chi^2 = 94.298$, $P < 0.001$; Glossy Swiftlet: $\chi^2 = 58.548$, $P < 0.001$; Fig. 4).

TABLE 2. Temporal (monthly) variation (%) in activities of Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Islands, India.

Species	Activity	Percentage time spent on an activity in respective months ($\bar{x}$ ± SD)						ANOVA	
		Jan	Feb	Mar	Apr	May	Jun	*F*	*P*
Edible-nest Swiftlet	Fly/glide	72.3 ± 22.2	69.4 ± 24.9	71.6 ± 17.2	75.9 ± 13.1	74.3 ± 11.9	81.1 ± 14.2	5.354	<0.001
	Feeding attempts	14.3 ± 15.2	16.7 ± 20.1	11.5 ± 10.6	14.3 ± 11.4	14.9 ± 9.6	13.2 ± 12.2	2.030	0.073
	Call	4.4 ± 8.0	1.7 ± 6.3	1.3 ± 2.8	1.4 ± 2.5	1 ± 2.8	2.1 ± 5.1	9.577	<0.001
	Follow	9.1 ± 16.3	12.7 ± 19.7	12.7 ± 13.1	8.5 ± 10.3	9.3 ± 9.4	4.7 ± 7	5.260	<0.001
	n = 719	n = 49	n = 63	n = 133	n = 211	n = 188	n = 75		
Glossy Swiftlet	Fly/glide	84.3 ± 18.4	78.9 ± 21.0	81.6 ± 18.6	89.4 ± 13.2	85.4 ± 15.6	91.6 ± 11.7	9.478	<0.001
	Feeding attempts	13.5 ± 18.0	19 ± 21.1	14.6 ± 18.5	10.3 ± 13.3	14.2 ± 15.3	7.6 ± 11.0	5.246	<0.001
	Call	0.9 ± 3.3	0.7 ± 3.7	1.9 ± 5.7	0	0.2 ± 1.5	0	15.654	<0.001
	Follow	1.3 ± 4.5	1.4 ± 5.3	1.9 ± 5.4	0.3 ± 1.8	0.3 ± 3.1	0.8 ± 4.5	9.042	<0.001
	n = 1,265	n = 210	n = 214	n = 238	n = 292	n = 252	n = 59		

TABLE 3. Temporal (hourly) variation (%) in activities of Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Islands, India.

Species	Activity	Time spent on an activity during different hours of the day ($\bar{x}$ ± SD)				ANOVA	
		0500–0815	0815–1130	1130–1445	1445–1800	*F*	*P*
Edible-nest Swiftlet	Fly/glide	73.4 ± 18.2	77.9 ± 16.1	76.4 ± 13.3	69.8 ± 13.6	8.764	<0.001
	Feeding attempts	13.1 ± 13.1	15.3 ± 13.9	13.3 ± 10.9	14.4 ± 9.6	1.245	0.292
	Call	2.3 ± 5.7	2.0 ± 5.8	1.4 ± 2.7	2.5 ± 4.7	1.352	0.256
	Follow	11.2 ± 14.9	4.9 ± 8.7	8.8 ± 9.6	13.3 ± 11.5	17.244	<0.001
	n = 719	n = 226	n = 194	n = 142	n = 157		
Glossy Swiftlet	Fly/glide	81.6 ± 18.1	85.1 ± 16.2	86.6 ± 16.1	85.6 ± 18.8	6.514	<0.001
	Feeding attempts	15.6 ± 17.9	12.7 ± 15.6	12.4 ± 16.0	14.1 ± 18.9	2.588	0.052
	Call	1.0 ± 3.6	1.0 ± 3.9	0.4 ± 3.3	0.2 ± 2.1	7.437	<0.001
	Follow	1.9 ± 6.0	1.3 ± 4.2	0.6 ± 3.2	0.06 ± 0.6	14.310	<0.001
	n = 1,265	n = 352	n = 324	n = 299	n = 290		

TABLE 4. Spatial variation (%) in activities of Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Islands, India.

Species	Activity	Time spent on an activity at different locations ($\bar{x}$ ± SD)				ANOVA	
		Hill base	Hill top	Open land-I	Open land-II	*F*	*P*
Edible-nest Swiftlet	Fly/glide	74.8 ± 15.1	72.9 ± 15.8	79.3 ± 20.8	73.9 ± 13.3	3.069	0.027
	Feeding attempts	13.7 ± 10.9	12.4 ± 10.6	20.7 ± 20.8	26.1 ± 13.3	13.390	<0.001
	Call	2.4 ± 5.9	2.3 ± 4.6	0	0	5.130	0.002
	Follow	9.1 ± 11.4	12.4 ± 13.2	0	0	24.400	<0.001
	n = 719	*n* = 333	*n* = 306	*n* = 67	*n* = 13		
Glossy Swiftlet	Fly/glide	90.4 ± 13.6	90.3 ± 14.9	74.00 ± 17.8	79.9 ± 18.6	57.552	<0.001
	Feeding attempts	7.4 ± 12.2	6.7 ± 12.9	25.90 ± 17.7	19.8 ± 18.6	152.767	<0.001
	Call	1.0 ± 4.6	1.2 ± 3.8	0.03 ± 0.6	0.05 ± 0.5	14.502	<0.001
	Follow	1.2 ± 4.9	1.9 ± 5.4	0.10 ± 1.2	0.20 ± 1.5	18.562	<0.001
	n = 1,265	*n* = 359	*n* = 411	*n* = 358	*n* = 137		

Statistically, monthly variations in feeding attempts could not be shown for Edible-nest Swiftlets for Inside Stream Bank Canopy, Inside Forest Canopy, and 0–5 m Above Ground categories and for Glossy Swiftlets in Below Stream Bank Canopy. The Edible-nest Swiftlet had monthly variations in feeding attempts except in 5–30 m Above Ground. The Glossy Swiftlet had monthly variations in 0–10 m Above Forest Canopy, Inside Forest Canopy, 0–10 m Above Stream Bank Canopy, and Inside Stream Bank Canopy (Table 9). Statistically, diurnal variations in feeding attempts could not be shown for Edible-nest Swiftlets in Inside Forest Canopy, Inside Stream Bank Canopy, Below Stream Bank Canopy, and 0–5 m Above Ground, and for Glossy Swiftlets in Below Stream Bank Canopy. The Edible-nest Swiftlet had significant diurnal variations in feeding attempts in 0–10 m Above Stream Bank Canopy, >30 m Above Ground, and 5–30 m Above Ground microhabitats, whereas the Glossy Swiftlet had diurnal variations, except in >10 m Above Forest Canopy, 0–10 m Above Forest Canopy, and >30 m Above Ground microhabitats (Table 10).

All microhabitats except Inside Forest Canopy and Inside Stream Bank Canopy were shared by the two species. Variations in microhabitat use could not be calculated for >10 m Above Forest Canopy, Inside Forest Canopy, Inside Stream Bank Canopy, >30 m Above Ground, and 0–5 m Above Ground. Both species had variations in use of microhabitats 0–10 m Above Forest Canopy, 0–10 m Above Stream Bank Canopy, and 5–30 m Above Forest Ground (Table 11). Important microhabitats for Edible-nest Swiftlets in descending order were >10 m Above Forest Canopy, >30 m Above Ground, and Above Forest Canopy. Inside Forest Canopy and Inside Stream Bank Canopy were important microhabitats for Glossy Swiftlets.

Foraging activities for both species were not correlated to mean temperature (Edible-nest Swiftlet: $r = 0.096$, $P = 0.856$; Glossy Swiftlet: $r = 0.007$, $P = 0.989$) and average rainfall (Edible-nest Swiftlet: $r = -0.447$, $P = 0.375$; Glossy Swiftlet: $r = -0.216$, $P = 0.682$).

TABLE 5. Variations ($\bar{x}$ ± SD, %) in feeding maneuvers by Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Island, India.

Feeding maneuver	Edible-nest Swiftlet *n* = 587	Glossy Swiftlet *n* = 673	Mann-Whitney test	
			Z	*P*
Twist	44.12 ± 47.44	61.29 ± 31.26	−4.347	<0.001
Fly-pause	2.43 ± 8.82	0.17 ± 1.59	−9.149	<0.001
Roll	2.40 ± 9.59	0.15 ± 1.43	−8.053	<0.001
Flutter	25.57 ± 23.26	19.28 ± 23.85	−3.516	<0.001
Tail-wing-open	25.48 ± 22.92	19.11 ± 23.83	−3.619	<0.001

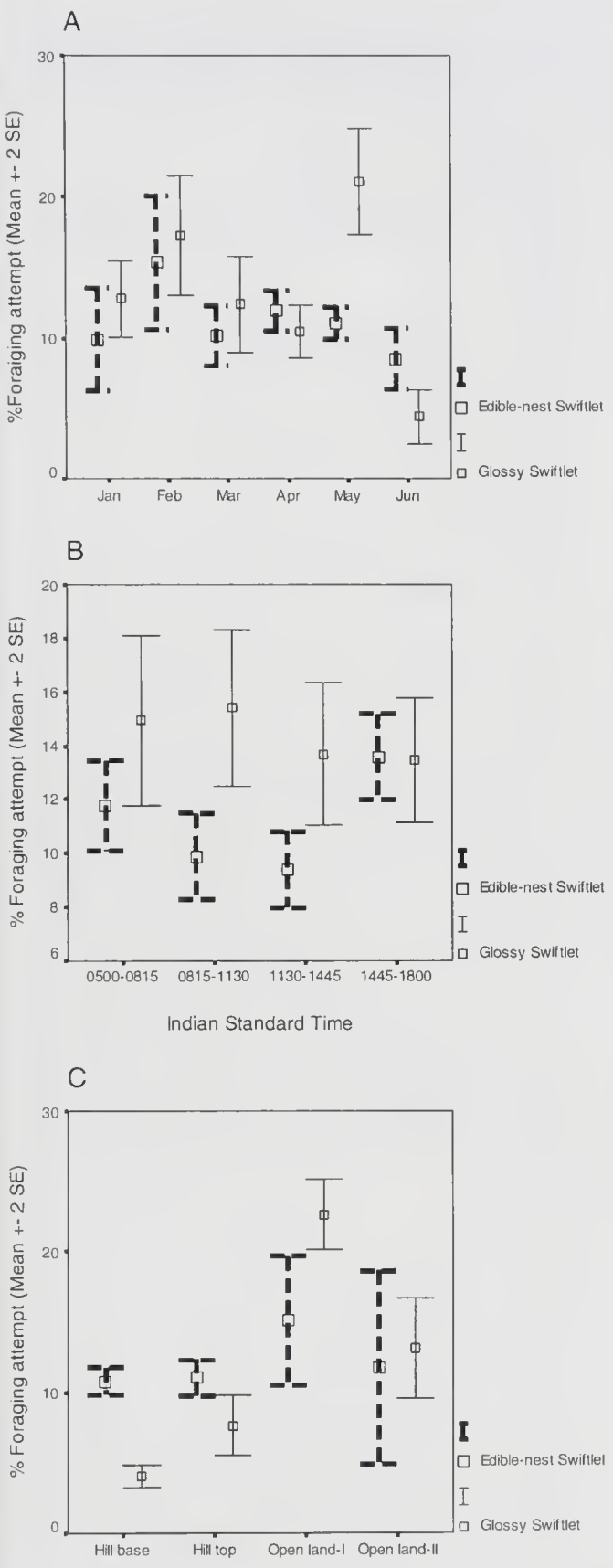

FIG. 2. Spatio-temporal variation (A = monthly, B = diurnal, and C = location; %) in feeding attempts of Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Island, India.

DISCUSSION

Aerial and Foraging Behavior.—Edible-nest and Glossy swiftlets performed fly/glide, foraging attempts (twist, fly-pause, roll, flutter, and tail-wing-open), call, follow, preen, defecate, and carry nest material in decreasing order. When breeding seasonality of the Edible-nest Swiftlet based on Sankaran and Manchi (2008), and Manchi (2009) was considered, temporal variations in activities of the two species near caves used for breeding appeared to be related to timing of breeding. Swiflets at Chalis-ek had chicks and eggs in the nest during April and May, and were more active near breeding sites. Edible-nest Swiftlets near caves used for breeding were inactive between 0700 and 1700 hrs, and 0800 and 1400 hrs, respectively, during early and late nest construction periods. Not requiring nest material might have led Edible-nest Swiftlets to spend most of the time exploring potential foraging areas away from breeding sites. Commencement of egg-laying during February followed by incubation, and brooding and feeding nestlings led to increased activity of Edible-nest Swiftlets near breeding sites. The active period of Edible-nest Swiftlets declined after May (Fig. 1), which was attributed to fledging occurring from most nests and avoidance of extreme weather conditions (Medway 1962).

Medway (1962) reported wider foraging ranges of Edible-nest Swiftlets in the non-breeding season, leading to changes in activity near breeding sites. Swiftlets at Chalis-ek, traveled away from the caves even during the pre-incubation period, possibly due to non-availability of food near caves. Food availability for swiftlets depends on the density and diversity of insects which in turn depend on weather conditions (Johnson 1969). Glossy Swiftlets were more active in early and late morning hours, but did not have significant diurnal variations in activities (Fig. 2). Asynchronous breeding in the Andaman and Nicobar Islands by Glossy Swiftlets may have resulted in no variation in diurnal activities.

Fly/glide was the most frequent behavior apparently used for scanning foraging areas while traveling to other foraging areas. Both species spent substantial time in fly/glide which depends on availability of insects. Insect density varies chronologically, spatially, and seasonally (Johnson 1969), thus, affecting fly/glide in the two species. Feeding attempt was the second major

TABLE 6. Temporal (monthly) variation (%) in foraging maneuvers of Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Islands, India.

Species	Foraging maneuvers	Time spent on different foraging maneuvers in respective months ($\bar{x}$ ± SD)						ANOVA	
		Jan	Feb	Mar	Apr	May	Jun	*F*	*P*
Edible-nest Swiftlet	Twist	65.4 ± 30.5	46.9 ± 33.4	40.5 ± 29.2	45.7 ± 25.4	42.0 ± 23.8	36.2 ± 29.2	5.564	<0.001
	Fly-pause	5.2 ± 9.4	6.8 ± 17	5.7 ± 14.2	0.8 ± 3.1	0.5 ± 1.8	3.7 ± 11.0	12.108	<0.001
	Roll	0	4.4 ± 8.7	7.2 ± 19.7	1.3 ± 4.6	1.1 ± 4.8	1.8 ± 6.7	7.740	<0.001
	Flutter	22.3 ± 21.6	32.6 ± 31.4	23.5 ± 24.8	24.3 ± 22.8	26.7 ± 19.3	26.8 ± 27.3	1.331	0.249
	Tail-wing-open	7.1 ± 11.9	9.3 ± 11.8	23.1 ± 22.4	27.8 ± 21.7	29.8 ± 23.6	31.5 ± 26.4	12.112	<0.001
	n = 587	n = 33	n = 41	n = 97	n = 193	n = 173	n = 50		
Glossy Swiftlet	Twist	71.0 ± 30.5	69.2 ± 27.1	63.2 ± 33.2	59.2 ± 33	48.1 ± 26.8	60.9 ± 36.4	7.885	<0.001
	Fly-pause	0.9 ± 3.8	0	0.08 ± 0.9	0	0.04 ± 0.2	0	7.961	<0.001
	Roll	0.3 ± 2.3	0.3 ± 1.9	0.3 ± 1.7	0	0	0	1.617	0.153
	Flutter	20.3 ± 25.5	14.5 ± 18.4	15.7 ± 22.2	19.5 ± 25.5	23.6 ± 22.4	30.7 ± 36.9	4.395	<0.001
	Tail-wing-open	7.5 ± 14.7	16.0 ± 19.6	20.7 ± 27.3	21.2 ± 26.1	28.2 ± 23.2	8.5 ± 17.9	12.588	<0.001
	n = 673	n = 102	n = 121	n = 131	n = 151	n = 143	n = 25		

TABLE 7. Temporal (hourly) variation (%) in foraging maneuvers of Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Islands, India.

Species	Foraging maneuvers	Time spent on different foraging maneuvers during different hours of the day ($\bar{x}$ ± SD)				ANOVA	
		0500–0815	0815–1130	1130–1445	1445–1800	*F*	*P*
Edible-nest Swiftlet	Twist	44.2 ± 27.7	48.9 ± 27.4	41.5 ± 26.8	40.9 ± 26.8	1.861	0.135
	Fly-pause	3.4 ± 11.2	1.3 ± 4.7	1.8 ± 6.4	3.0 ± 10.5	2.246	0.082
	Roll	1.4 ± 9.0	2.0 ± 9.1	3.7 ± 15.2	3.0 ± 8.0	1.230	0.298
	Flutter	29.3 ± 24.0	23.6 ± 24.3	23.4 ± 22.6	25.1 ± 21.5	2.176	0.090
	Tail-wing-open	21.6 ± 22.0	24.3 ± 23.6	29.6 ± 24.7	28.1 ± 20.9	3.283	0.021
	n = 587	n = 172	n = 155	n = 121	n = 139		
Glossy Swiftlet	Twist	65.4 ± 29.7	59.1 ± 33.1	56.9 ± 32.9	62.4 ± 28.8	2.380	0.069
	Fly-pause	0.2 ± 2.1	0.1 ± 1	0.3 ± 1.9	0.03 ± 0.3	0.691	0.558
	Roll	0	0.08 ± 1.1	0.6 ± 2.7	0	7.209	<0.001
	Flutter	18.7 ± 22.9	16.4 ± 22.4	20.9 ± 26.4	21.7 ± 23.7	1.652	0.176
	Tail-wing-open	15.7 ± 20.7	24.2 ± 27.1	21.4 ± 24.3	15.8 ± 22.2	4.802	0.003
	n = 673	n = 211	n = 167	n = 152	n = 143		

TABLE 8. Spatial variations in the proportionate activities of Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Island, India ($P < 0.05$ = significant difference).

Species	Foraging maneuvers	Time spent on different foraging maneuvers at different locations ($\bar{x} \pm$ SD)				ANOVA	
		Hill base	Hill top	Open land-I	Open land-II	F	P
Edible-nest Swiftlet	Twist	43.0 ± 25.5	42.4 ± 27.6	56.6 ± 31.4	63.0 ± 35.0	5.977	<0.001
	Fly-pause	2.4 ± 8.8	2.4 ± 9.3	2.8 ± 6.9	2.4 ± 5.0	0.248	0.863
	Roll	1.5 ± 7.8	3.3 ± 11.6	3.2 ± 7.6	0.6 ± 2.1	2.147	0.093
	Flutter	26.5 ± 20.7	25.2 ± 25.6	21.7 ± 23.4	25.8 ± 26.4	1.141	0.332
	Tail-wing-open	26.6 ± 22.8	26.8 ± 23.3	15.7 ± 19.6	8.5 ± 11.5	4.844	0.002
	n = 587	n = 276	n = 256	n = 42	n = 13		
Glossy Swiftlet	Twist	65.7 ± 36.9	69.3 ± 33.6	56.5 ± 25.7	58.9 ± 32.4	6.407	<0.001
	Fly-pause	0.3 ± 2.8	0	0.2 ± 1.4	0.07 ± 0.4	1.127	0.337
	Roll	0.1 ± 1.2	0.2 ± 1.4	0.2 ± 1.7	0	0.725	0.537
	Flutter	21.1 ± 31.9	14.4 ± 25.9	20.2 ± 18.6	20.3 ± 21.4	4.553	0.004
	Tail-wing-open	12.7 ± 25.3	16.1 ± 26.0	22.9 ± 20.6	20.7 ± 25.9	11.288	<0.001
	n = 673	n = 141	n = 134	n = 306	n = 92		

activity after fly/glide. All individual activities, except feeding attempts, had temporal variations in their proportions by month. No diurnal variation in feeding attempts and calls was recorded. Call and follow were presumed to be mating/pairing displays as well as a response to foraging competition. Call and follow activities by Edible-nest Swiftlets, and follow by Glossy Swiftlets were higher during nest construction (Jan–Feb). This suggests that follow must be more related to mating.

Insect diversity was assumed to affect the occurrence of different foraging maneuvers with the presumption that different foraging maneuvers are used to prey on different type of insects. This dependence resulted in temporal (monthly and hourly) variations in the proportions of different foraging maneuvers.

One factor considered was that Glossy Swiftlets have been shown to be more maneuverable than Edible-nest Swiftlets (Tarburton 1986), as it has both a higher wing and tail maneuverability index. This could help explain why Glossy Swiftlets were able to produce greater variability in feeding and flutter maneuvers. Roll alone by Glossy Swiftlets had diurnal variations; however, no diurnal variation was observed in foraging maneuvers by Edible-nest Swiftlets. Spatial variations were shown by twist and tail-wing-open in both species, and flutter alone by Glossy Swift-

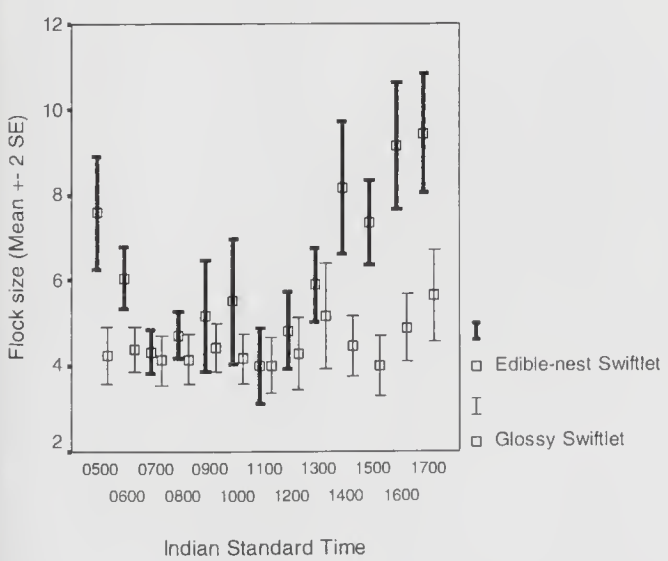

FIG. 3. Temporal variations in diurnal flock sizes of Edible-nest and Glossy swiftlets at Chalis-ek, North Andaman Island, India.

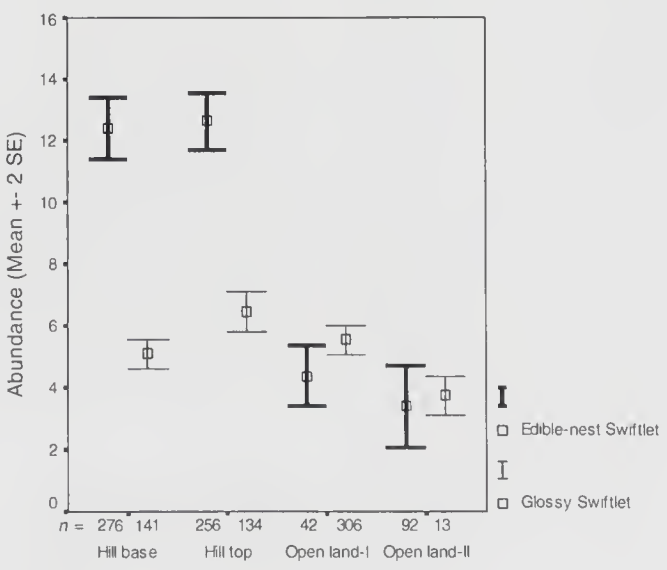

FIG. 4. Variation in abundance of Edible-nest and Glossy swiftlets at four locations at Chalis-ek, North Andaman Island, India.

TABLE 9. Temporal (monthly) variation (%) in feeding attempts of Edible-nest and Glossy swiftlets in different microhabitats at Chalis-ek, North Andaman Islands, India.

Species	Microhabitats	Time spent for feeding attempts in different microhabitats in respective months ($\bar{x} \pm$ SD)						Kruskal-Wallis test	
		Jan	Feb	Mar	Apr	May	Jun	χ^2	*P*
Edible-nest Swiftlet	>10 m Above Forest Canopy	64 ± 47.9	40.2 ± 49	69.8 ± 32.8	44 ± 35.1	36 ± 29.8	52 ± 28.4	43.128	<0.001
	0–10 m Above Forest Canopy	6.3 ± 16.8	39 ± 48.1	30.2 ± 32.8	50 ± 36.2	64 ± 29.8	48 ± 28.5	132.985	<0.001
	Inside Forest Canopy	0	0	0	0	0	0		
	0–10 m Above Stream Bank Canopy	10.9 ± 24.5	3.7 ± 13.2	0	0.3 ± 3.6	0	0	68.274	<0.001
	Inside Stream Bank Canopy	0	0	0	0	0	0		
	Below Stream Bank Canopy	1.6 ± 8.8	0	0	0	0	0		
	>30 m Above Ground	17.2 ± 37.3	14.6 ± 34	0	2.6 ± 14.2	0	0	56.374	<0.001
	5–30 m Above Ground	0	2.4 ± 15.6	0	2.3 ± 13.8	0	0	10.798	0.056
	0–5 m Above Ground	0	0	0	0.8 ± 6.2	0	0		
	n = 583	n = 32	n = 41	n = 96	n = 192	n = 172	n = 50		
Glossy Swiftlet	>10 m Above Forest Canopy	2.1 ± 14.3	0	0	0	0.3 ± 4.2	2 ± 10	10.552	0.061
	0–10 m Above Forest Canopy	29.4 ± 44.3	37.1 ± 45.9	40 ± 45.1	37.7 ± 44.9	25.1 ± 38.3	58 ± 31.2	33.855	<0.001
	Inside Forest Canopy	13.9 ± 32.9	27.7 ± 42.4	38.5 ± 44.7	8.4 ± 22.1	8.6 ± 19.8	40 ± 32.3	74.086	<0.001
	0–10 m Above Stream Bank Canopy	34 ± 46.5	19 ± 39.2	8.1 ± 27	22.3 ± 28.6	28.3 ± 27.3	0	97.277	<0.001
	Inside Stream Bank Canopy	7.2 ± 26	8.8 ± 27.7	6.9 ± 24.7	21.3 ± 29.3	31.1 ± 28.7	0	160.662	<0.001
	Below Stream Bank Canopy	1 ± 10.2	0	0	0	0	0		
	>30 m Above Ground	0.5 ± 5.1	0.3 ± 3.1	0	0.2 ± 2.7	0	0	2.547	0.769
	5–30 m Above Ground	11.3 ± 31	6.7 ± 23.7	6.5 ± 23.6	7.7 ± 22.5	6.2 ± 19.9	0	6.075	0.299
	0–5 m Above Ground	0.5 ± 5.1	0.4 ± 4.7	0	2.4 ± 11.4	0.3 ± 4.2	0	16.713	0.005
	n = 656	n = 97	n = 112	n = 130	n = 149	n = 143	n = 25		

TABLE 10. Temporal (diurnal) variations in activity of Edible-nest and Glossy swiftlets in different microhabitats at Chalis-ek, North Andaman Islands, India.

Species	Microhabitats	Time spent on feeding attempts during different hours of the day ($\bar{x} \pm$ SD)				Kruskal-Wallis test	
		0500–0815	0815–1130	1130–1445	1445–1800	χ^2	P
Edible-nest Swiftlet	>10 m Above Forest Canopy	45.9 ± 36.8	42.1 ± 36.4	51.2 ± 37.3	51.8 ± 35.4	6.255	0.10
	0–10 m Above Forest Canopy	50 ± 37.4	43.1 ± 36	48.8 ± 37.3	48.2 ± 35.4	2.168	0.538
	Inside Forest Canopy	0	0	0	0		
	0–10 m Above Stream Bank Canopy	0.9 ± 8.5	2.6 ± 11.2	0	0	15.846	0.001
	Inside Stream Bank Canopy	0	0	0	0		
	Below Stream Bank Canopy	0.3 ± 3.8	0	0	0		
	>30 m Above Ground	1.7 ± 12	8.9 ± 27.1	0	0	32.251	<0.001
	5–30 m Above Ground	1.2 ± 10.7	2.3 ± 13.3	0	0	8.563	0.036
	0–5 m Above Ground	0	1 ± 7	0	0		
	$n = 583$	$n = 172$	$n = 152$	$n = 121$	$n = 138$		
Glossy Swiftlet	>10 m Above Forest Canopy	0	0.6 ± 7.8	1.3 ± 9.9	0	7.001	0.072
	0–10 m Above Forest Canopy	32.8 ± 41.5	38.3 ± 44.7	34.4 ± 44.4	34 ± 44.8	1.865	0.601
	Inside Forest Canopy	28.1 ± 39.4	17.8 ± 33.9	11.9 ± 28.1	18.4 ± 35.6	17.271	0.001
	0–10 m Above Stream Bank Canopy	20.8 ± 37.5	17.2 ± 29	26 ± 35	20.9 ± 32.8	10.063	0.018
	Inside Stream Bank Canopy	8.5 ± 24	15.3 ± 26.9	22.1 ± 32.4	18.8 ± 30.8	29.471	<0.001
	Below Stream Bank Canopy	0.5 ± 7.1	0	0	0		
	>30 m Above Ground	0.5 ± 2.4	0.3 ± 3.9	0.2 ± 2.7	0	0.885	0.829
	5–30 m Above Ground	8.1 ± 25.3	8.8 ± 23.5	3.6 ± 17.4	7.8 ± 26.2	10.117	0.018
	0–5 m Above Ground	0.9 ± 8.2	1.7 ± 8.2	0.3 ± 4.1	0	10.114	0.018
	$n = 656$	$n = 199$	$n = 165$	$n = 151$	$n = 141$		

TABLE 11. Association between Edible-nest (ENS) and Glossy swiftlets (GS) with microhabitat use at Chalis-ek, North Andaman Island, India.

Microhabitat[a]	Species	*n*	Activity ($\bar{x}$ ± SD)	$\chi 2$	*P*
HaFC	ENS	412	11.47 ± 10.09	—	
	GS	4	6.75 ± 2.06		
AFC	ENS	413	11.43 ± 9.38	109.901	<0.001
	GS	277	8.32 ± 13.02		
IFC	ENS	0	0	—	
	GS	174	6.95 ± 7.53		
ASC	ENS	10	18.50 ± 13.19	228.748	<0.001
	GS	209	24.82 ± 20.74		
ISC	ENS	0	0	—	
	GS	169	24.07 ± 19.54		
BSC	ENS	1	39	0.009	0.923
	GS	1	12		
HaG	ENS	20	15.05 ± 12.53	—	
	GS	3	40.00 ± 26.00		
LaG	ENS	7	5.43 ± 5.29	48.672	<0.001
	GS	65	18.95 ± 22.84		
NG	ENS	3	7.00 ± 5.29	—	
	GS	11	17.64 ± 8.58		

[a] HaFC: >10 m Above Forest Canopy; AFC: 0–10 m Above Forest Canopy; IFC: Inside Forest Canopy; ASC: 0–10 m Above Stream Bank Canopy; ISC: Inside Stream Bank Canopy; BSC: Below Stream Bank Canopy; HaG: >30 m Above Ground; LaG: 5–30 m Above Ground; NG: 0–5 m Above Ground; — = cannot be calculated.

lets. Monthly variations in foraging maneuvers indicate significant seasonal variations in insect diversity and change in prey preference with breeding stages (Johnson 1969). Diurnal variation in insect diversity in the forest is uncertain, although differing slightly in open lands. This indicates that most foraging attempts in the microhabitats >10 m Above Forest Canopy and >30 m Above Ground may be because of more dispersion of insects at that height (Johnson 1969).

Habitats and Microhabitats.—Edible-nest Swiftlets were more active in forested areas, whereas Glossy Swiftlets were more active in open paddy lands. The Edible-nest Swiftlet's activity is in concordance with previous studies (Medway 1962, Harrison 1972, Hails and Amirrudin 1981, Waugh and Hails 1983, Charles 1987, Lim and Cranbrook 2002, Nguyen et al. 2002). The Glossy Swiftlet is the only swiftlet species known to occur in all habitats. The diet of the Glossy Swiftlet in Malaysia (Laurie and Tompkins 2000) shows elasticity in food and foraging habitat selection unlike the Edible-nest Swiftlet. Further validity is given the concept of greater elasticity by Collins (2000) for Glossy Swiftlets on Palawan where it has resource partitioning caused by the presence of Pygmy Swiftlet (*Collocalia troglodytes*). In this situation, it was restricted in most of its feeding to <2 m above ground; a zone more likely to increase vulnerability to land-based predators. That this species flies so low when "forced" into ecological partitioning was reported from New Guinea by Schoddle and Hitchcock (1968), where it was sharing habitat with the Uniform Swiftlet (*Aerodramus vanikorensis*). It has been shown on that same island, but at greater altitudes, to share space with the Mountain Swiftlet (*A. hirundinaceus*) in a similar way (Diamond 1972).

Edible-nest Swiftlets were more active in early morning and late afternoon and were in larger foraging flocks near caves used for breeding. Frequency of feeding attempts by both species was correlated with foraging flock size.

Edible-nest Swiftlets forage high above the canopy, while Glossy Swiftlets forage at the canopy level and near the ground. Johnson (1969) suggested that insects move upwards in air with an increase in ambient temperature. This may be the reason for the shift of Edible-nest Swiftlets to higher altitudes during foraging and Glossy Swiftlets, being smaller and more agile to maneuver in confined spaces, to move towards relatively cooler zones inside the canopy at the forest edges or stream banks close to open paddy lands for foraging.

Variations in microhabitat use signify resource partitioning among Edible-nest and Glossy swift-

lets at Chalis-ek with Edible-nest Swiftlets having affinity for categories, >10 m Above Forest Canopy, >30 m Above Ground, and Above Forest Canopy, and Glossy Swiftlets for Inside Forest Canopy and Inside Stream Bank Canopy in descending order. Variations in foraging maneuvers indicate variations in food preferences by both species as demonstrated by gut content and bolus analysis (Medway 1962, Harrison 1972, Hails and Amiruddin 1981, Waugh and Hails 1983, Charles 1987, Collins 2000, Laurie and Tompkins 2000). The Edible-nest Swiftlet's affinity towards >30 m Above Ground in open land for foraging was unusual as the species has been known to prefer forested areas. The plasticity in food selection by Edible-nest Swiftlets (Charles 1987, Laurie and Tompkins 2000) suggests two microhabitats, >10 m Above Forest Canopy and >30 m above ground, may have similar insect diversity. This demonstrates that forested habitat and microhabitats above forest canopy level are important for Edible-nest Swiftlets. Glossy Swiftlets also had affinity towards both available habitats.

We infer, in concurrence with previous studies, that cave-dwelling Edible-nest Swiftlets are dependent on forests and will be adversely affected by the present rate of deforestation and habitat alteration. Changes in land use away from caves used for breeding sites will also lead to population declines of Edible-nest Swiftlets because of its wider foraging ranges. However, habitat alteration around breeding caves may not have a marked effect on foraging activities of Glossy Swiftlets, which have more elasticity in habitat use.

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GOLDEN- AND BLUE-WINGED WARBLERS: DISTRIBUTION, NESTING SUCCESS, AND GENETIC DIFFERENCES IN TWO HABITATS

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ABSTRACT.—We analyzed phenotypic distribution, nesting success, and genetic purity of Golden-winged Warblers (*Vermivora chrysoptera*) and Blue-winged Warblers (*V. pinus*) in two ecologically distinct nesting habitats: early-succession uplands, and swamp forests. The proportion of phenotypically pure Golden-winged Warblers in swamp forests (94%) differed significantly from uplands (53%) as did the proportion of Golden-winged Warbler pairs (93%) in swamp forests compared to uplands (48%). Only 1% of the phenotypically pure Golden-winged Warblers in swamp forests paired with either a hybrid or a Blue-winged Warbler, but 7% of the phenotypically pure Golden-winged Warblers in uplands formed a hybrid pair. The probability of nesting success for Golden-winged Warbler pairs in swamp forests (65%) was significantly higher than in uplands (37%). Mitochondrial DNA analyses indicate that all 10 phenotypically pure Golden-winged Warblers sampled from swamp forests had the ancestral Golden-winged Warbler haplotype, while 10 of 25 Golden-winged Warblers from uplands had the ancestral Blue-winged Warbler haplotype ($P = 0.033$). Swamp forests may provide a source habitat for Golden-winged Warblers with a high phenotypic and genotypic purity even in sympatry with Blue-winged Warblers. *Received 27 August 2009. Accepted 23 December 2009.*

The Golden-winged Warbler (*Vermivora chrysoptera*) has declined 8.8% per year in U.S. Fish and Wildlife Region 5 from 1966 to 2007 (Sauer et al. 2008). This decline occurred in all areas that surround the site for this study, Sterling Forest State Park, New York, USA. The Golden-winged Warbler declined by 53 and 72% in New York (Confer 2008) and in Pennsylvania (Pennsylvania Breeding Bird Atlas 2009), respectively, during the last 20 years. This species has declined from ~200 pairs to 15 pairs in New Jersey from 1998 to 2008, according to statewide surveys by the New Jersey Division of Fish and Wildlife (S. M. Petzinger, unpubl. data). The Golden-winged Warbler has been extirpated in Massachusetts and greatly declined in Connecticut following intrusion by the Blue-winged Warbler (*V. pinus*) despite 14,000 ha of suitable shrubland habitat on utility rights-of-ways (Confer and Pascoe 2003). Population declines of the Golden-winged Warbler usually follow arrival of the Blue-winged Warbler with subsequent competition and hybridization (Confer et al. 2003). However, Golden-winged Warblers have co-existed with Blue-winged Warblers for over a century (Eaton 1914) in southern New York and populations appear to be stable at ~125 breeding pairs in Sterling Forest State Park (Confer et al. 1998, this study).

Initial surveys in 1999 and 2000 were conducted in uplands, where both Golden-winged and Blue-winged warblers occur frequently. It became apparent that both species also nested in two wetland communities described by the New York State Natural Heritage Program (Reschke 1990). The shrub swamp community supported about equal numbers of both species. The red maple (*Acer rubrum*) hardwood forest community, or swamp forest, attracted primarily Golden-winged Warblers and our wetland surveys focused on this habitat.

This study tests the hypothesis that favorable demographics for Golden-winged Warblers in swamp forest habitat account for its long-term stability and its co-existence with Blue-winged Warblers in Sterling Forest State Park, New York. Specifically, we hypothesize that Golden-winged Warblers will have higher nesting success, lower hybridization rates, and higher genetic purity in swamp forest habitats than in uplands.

METHODS

The principal author and a field crew of three to seven people studied Golden-winged and Blue-winged warblers for 5 to 6 days a week for 10 weeks in Sterling Forest State Park, New York in 2001, 2003–2006, and 2008. Territories of Golden-winged and Blue-winged warblers often were contiguous or overlapped and, at times, data could be acquired by sound from more distant territories. Each territory was observed for 25–100 person-hrs based on 15–50 person-visits, including simultaneous observation of more than one

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territory. Male Golden-winged Warblers were banded as early in the season as possible to assist delineation of territorial boundaries and pairing status. At least 80% of the males were individually recognizable within 3 weeks of the start of the season, assisted by a ~50% return rate of banded males and distinctive phenotypes of occasional hybrids. The intervals between observations were too long to be used for calculations of nesting success during 2002 and 2007. We included observations from 2002 to help estimate the number of birds and their phenotype in different habitats.

We made observations each year in 3–4 upland sites separated by 8–14 km, and 5–12 swamp forests separated by 4–12 km, depending on size of the field crew. We tried to obtain complete demographic values and blood samples for every pair in every patch, which provide an unbiased estimate of demographic values within each patch. Sites were selected because they had typical habitat and provided a large number of *Vermivora* territories in a contiguous area, facilitating data collection.

Upland sites consisted of a segment of rights-of-way (ROW) with a managed width of ~20 m, another ROW segment with ~80 m of managed width, a managed successional field, and an unmanaged area of secondary succession. These sites provide the total range of upland habitat used by *Vermivora* in the park. The two ROW sites were the only segments of ROW that provided continuous habitat with eight or more adjacent or over-lapping *Vermivora* territories. We estimate the upland sites we sampled probably supported more than half of all upland *Vermivora* territories in the park based on Geographic Information System (GIS)-based habitat classification of satellite imagery, surveys along all ROW in the park, and our visits to many small patches of disturbance habitat. Both ROWs have been managed in a stable vegetative condition for the last 40 years by a combination of herbicide application and cutting. Both ROW have about 60% herb cover.

The two upland successional sites used for this study had ~9–12 ha of successional habitat. One of the upland sties has been used for experimental habitat management for Golden-winged Warblers and this management created early secondary succession habitat. The second successional site was an abandoned gravel mine with secondary succession field/shrub conditions. Most of the habitat used by *Vermivora* at this site was flooded by a large American beaver (*Castor canadensis*) pond built in summer 2006. Monitoring at this site has ended.

All swamp forest patches were between ~0.5 and 5 ha and supported 1–3 pairs of *Vermivora*. We monitored 12 patches of swamp forest, summed for all years, which provided a representative sample of *Vermivora* demographics for swamp forests in general.

Nests were observed at 2–5 day intervals. We visited nests more frequently when nestlings were expected to be 5–7 days of age and appropriate for blood sampling and near the time of fledging. Estimation of nesting success followed Mayfield (1961). We calculated nesting success starting with the first day of incubation, assuming incubation lasted 11 days and the nestling stage lasted 10 days. Many nests discovered during construction or egg-laying were abandoned. We attributed most of the high failure rate early in the nesting cycle to human-induced abandonment and omitted these nests from calculations of nest success. We found six second nest attempts of pairs whose first nest was predated after incubation started. These re-nests are included in the sample size for nests.

We used the criteria of Gill (1980) to distinguish between phenotypically pure and hybrid birds. We used Chi-square, 2×2, contingency tests with Yeats correction for continuity with larger samples to test for differences in the distribution of pure and hybrid phenotypes in upland and swamp forests, and Fisher's exact probability value for tests where some cells had expected values <5. We used a t-test to compare the probability of nesting success between upland and swamp forest habitats.

Mitochondrial DNA analyses of Golden-winged and Blue-winged warblers show little variation within two distinct haplotypes, presumably the ancestral mtDNA of each species. The two haplotypes differ from each other by 3–5% (Gill 1997, Shapiro et al. 2004, Dabrowski et al. 2005). Samples from Sterling Forest State Park collected in 2002 and 2003 showed extensive introgression with 12 of 28 phenotypically pure Golden-winged Warblers having the ancestral Blue-winged Warbler haplotype (Dabrowski et al. 2005). P. J. Hartman (pers. comm.), continuing mtDNA analyses of Sterling Forest State Park samples, found the same haplotype classification for four replicate samples analyzed by both

TABLE 1. Abundance of resident warbler pairs by phenotypes in swamp forests and uplands in Sterling State Park Forest, New York, 2001–2006 and 2008.

Habitat	Male and female phenotypes of pairs, males listed first						
	GW[a] × GW	BR × GW	GW × BR	GW × BW	BW × BW	BW × GW	BR × BW
Swamp forests	42	1	0	0	2	0	0
Uplands	46	2	3	1	40	1	2

[a] Abbreviations: GW = Golden-winged Warbler, BR = Brewster's Warbler (hybrid), and BW = Blue-winged-Warbler.

laboratories. Pooling results from these two laboratories, we compare the phenotype-haplotype concordance of 35 phenotypically pure Golden-winged Warbler individuals in upland and swamp forest habitats in Sterling Forest State Park.

RESULTS

All upland sites included herbaceous patches of goldenrod (*Solidago* spp.) and grasses, and shrub patches of dogwood (*Cornus* spp.) and briers (*Rubus* spp.). Poison ivy (*Toxocodendron radicans*) and Asiatic bittersweet (*Celastrus orbiculatus*) were widely distributed and, at times, formed dense stands. Forests formed at least half of the boundary for all upland territories. Results from upland sites were pooled because vegetation varied as much within one site as among the sites, and because inspection of our data did not suggest any difference in population parameters among these sites. Red maple dominated the canopy in swamp forests of Sterling Forest State Park, and provided ~60–80% canopy closure. Dead tree trunks suggest that elms (*Ulmus* spp.) were once dominant. Spice bush (*Lindera benzoin*) was the most widely distributed shrub followed in abundance by arrowwood (*Viburnum recognitum*) and wild raisin (*V. cassinoides*). Poison sumac (*Toxocodendron vernix*) and swamp azalea (*Rhododendron viscosum*) occurred occasionally. Tussock sedge (*Carex stricta*) strongly dominated the herb layer and was the principal substrate for nests in wetlands. Dense patches of *Phragmites* occurred in several locations, although Golden-winged Warblers seldom perched on this plant and only once used it as a nest substrate. Data from all swamp forests were pooled for the same reasons applied to the upland sites.

Phenotypically pure Golden-winged Warblers during 2001–2006, and 2008 comprised 94% (85 of 90) of the resident individuals in swamp forests and 53% (99 of 186) in uplands (Table 1) (X^2 = 43.97; df = 1, $P < 0.001$). The proportion of Golden-winged Warbler individuals in these two habitats was reflected in pairings among the pure and hybrid phenotypes. Phenotypically pure Golden-winged Warblers formed 93% (42 of 45) of all pairs in swamp forests but only 48% (46 of 95) in uplands (X^2 = 23.81; df = 1, $P < 0.001$). The rate of introgression due to hybrid pairings was marginally lower in swamp forests. Only 1% (1 of 85) of the phenotypically pure Golden-winged Warbler individuals formed a social pair with either a hybrid or a Blue-winged Warbler in swamp forests, but 7% (7 of 99) of the phenotypically pure Golden-winged Warblers formed a hybrid pair in uplands (Fisher's exact one-tailed test; df = 1, $P = 0.051$).

The probability of nesting success in uplands varied considerably among years and between Golden-winged and Blue-winged warblers (Table 2). This large variation may be partially due to differences in predator abundance, although the variation is certainly partially due to the small sample of nests per habitat per year. Eastern chipmunks (*Tamias striatus*) were at least common on ROW, and became abundant following oak (*Quercus* spp.) mast years when as many as five to 10 chipmunks were often observed concurrently in 2002 and 2004. Black rat snakes (*Elaphe obsoleta*) were consistently common on ROW, probably due to the warming effect of direct sunshine and the presence of shelter in exposed rock talus. In contrast, no chipmunks or black rat snakes were observed in swamp forests during this study. The abundance of these predators on most ROW in Sterling Forest State Park may account for the variable and comparatively low nesting success of Golden-winged Warblers in uplands.

The estimated probability of nesting success for 2001, 2003–2006, and 2008 (Table 2) for Golden-winged Warblers in swamp forests (65% of 23 nests) was greater than in uplands (37% of 32 nests) (one-tailed *t*-test; df = 1, $P < 0.0485$). Nesting success for Blue-winged Warblers in uplands was moderately high at 54% based on 28

TABLE 2. Probability of nesting success for pairs of Golden-winged Warblers and Blue-winged Warblers in Sterling State Park Forest, New York. Six re-nests are included.

Year	Golden-winged × Golden-winged Warblers		Blue-winged × Blue-winged Warblers	
	Swamp forest	Upland	Swamp forest	Upland
2001	1[a] (3[b]/3[c])	0.49 (4/4)	0	1 (2/2)
2003	0.37 (3/3)	0.7 (7/7)	1 (1/1)	0.34 (3/3)
2004	0.59 (3/3)	0.26 (5/5)	0	0.29 (5/5)
2005	0.57 (6/6)	0.29 (4/4)	0	0.77 (5/4)
2006	0.82 (6/6)	0.23 (9/7)	0.21 (2/1)	0.61 (10/9)
2008	0.44 (2/1)	0.32 (3/3)	0	0.42 (3/3)
Totals	0.65 (23/22)	0.37 (32/30)	0.42 (3/2)	0.54 (28/26)

[a] Probability of nesting success (Mayfield 1961).
[b] Number of nests.
[c] Number of pairs.

nests, but not significantly better than for Golden-winged Warblers. The low value for nesting success of Blue-winged Warblers in swamps (Table 2) is based on only three nests and is not reliable.

We collected >300 blood samples from adults and sets of nestlings to ascertain if swamp forests attracted a population of birds with greater genetic purity than uplands. Preliminary analyses of mitochondrial DNA indicate swamp forests support a higher proportion of Golden-winged Warbler phenotype-haplotype matches than upland habitat. All 10 phenotypically pure Golden-winged Warblers from swamp forests that have been analyzed had the ancestral Golden-winged Warbler haplotype, while 10 of 25 of the phenotypically pure Golden-winged Warblers from uplands had the ancestral Blue-winged Warbler haplotype (Table 3). These preliminary results strongly suggest swamp forests support a higher proportion of Golden-winged Warbler phenotype-haplotype matches than upland habitat.

DISCUSSION

Golden-winged Warblers expanded into the Northeast during the last 150 years, primarily into secondary succession shrublands on abandoned farmland and most of the populations now nest in the North Central states, often on clear cut timberlands (Gill 1980, Huffman 1997). Studies throughout the Golden-winged Warbler range describe use of anthropogenic, disturbance ecosystems on dry sites: e.g., Georgia (Klaus and Buehler 2001), northcentral New York (Confer et al. 2003), Pennsylvania (Kubel 2005; J. L. Larkin, unpubl. data), Virginia (Wilson et al. 2007), West Virginia (Canterbury and Stover 1999), and Wisconsin (Roth and Lutz 2004). However, other studies have found nesting by Golden-winged Warblers in wetlands: Michigan (Berger 1958), southern New York (this study), North Carolina (Rossell et al. 2003), and northern New York according to surveys by the New York State Department of Environmental Conservation (T. Q. Rush and T. J. Post, unpubl. data). Some speculate the historical abundance of beaver meadows and other wetlands provided the evolutionary crucible (Hunter et al. 2001).

Both wet and dry Golden-winged Warbler territories are dominated by patches of herbs and shrubs and, usually, a forested boundary. Upland sites with these attributes have been described for central New York (Confer and Knapp 1981), northcentral New York (Confer et al. 2003), southern New York (this study), and clearcuts in Georgia (Klaus and Buehler 2001). GIS mapping of vegetation has shown Golden-winged Warbler territories include a diverse mosaic of successional habitat types, especially herbaceous openings, and are often surrounded by forest in a wetland in North Carolina (Rossell et al. 2003), and in wet and dry territories in Sterling Forest State Park (J. L. Confer and J. L. Larkin, unpubl. data). Wetlands with many patches of vegetation in both southern New York (this study) and northern New York, according to surveys by the New York State Department of Environmental Conservation (T. Q. Rush and T. J. Post, unpubl. data), attracted a nearly pure Golden-winged Warbler population despite the presence of Blue-winged Warblers in nearby uplands.

Our multi-year observations in Sterling Forest State Park overcome extreme annual variation and show major differences in population demograph-

TABLE 3. Distribution of ancestral Golden-winged or Blue-winged warbler mitochondrial DNA for birds with pure Golden-winged Warbler phenotype nesting in two habitats.

Habitat	Mitochondrial haplotype	
	Golden-winged Warbler	Blue-winged Warbler
Swamp Forests	10	0[a]
Uplands	15	10

[a] Fisher's exact probability test; P for two-tailed test = 0.033.

ics between wet and dry habitats. The proportion of Golden-winged Warblers to Blue-winged Warblers and hybrid phenotypes is much higher in swamp forests than in uplands. The absence of ancestral Blue-winged Warbler mtDNA in the sample of phenotypically pure Golden-winged Warblers in swamp forests indicates a history of infrequent hybridization for Golden-winged Warblers in swamp forests. We observed a low frequency of hybrid pairings in swamp forests, which suggests the current rate of introgression is also lower in swamp forests than in uplands. Further, nesting success in swamp forests was ~75% better than nesting success in uplands. Our results strongly indicate the unusual persistence of Golden-winged Warblers in the presence of Blue-winged Warblers in uplands of Sterling Forest State Park is the result of a source/sink dynamic between swamp forests and uplands.

Continued stability of genetically pure Golden-winged Warblers in this region may require that swamp forests sustain a sufficiently large population to buffer stochastic events. We observed about 55 Golden-winged Warbler pairs during casual surveys in 2009 with 22 pairs in swamp forests. We extrapolate, using GIS-based habitat classification, to an estimate of ~125 Golden-winged Warbler pairs in Sterling Forest State Park with ~50 in swamp forests. The Sterling Forest State Park population alone may be too small to perpetuate the Golden-winged Warbler. Fortunately, Sterling Forest State Park is within the Hudson Highlands, a tri-state parkland of 28,000 ha. Red maple hardwood forests occur throughout this larger area. Management for swamp forests throughout the larger Hudson Highlands could help sustain the Golden-winged Warbler population in this region. The presence of Golden-winged Warblers in wetlands with a mosaic of vegetation in North Carolina and southern and northern New York with habitat segregation from Blue-winged Warblers in the New York studies may provide important examples for management in a wide area of sympatry. Further analyses of genetic purity and population demographics comparing uplands and wetlands would be valuable.

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GENETIC AND MORPHOLOGICAL VARIATION OF THE SOOTY-CAPPED BUSH TANAGER (*CHLOROSPINGUS PILEATUS*), A HIGHLAND ENDEMIC SPECIES FROM COSTA RICA AND WESTERN PANAMA

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ABSTRACT.—We examined the effect of geographic isolation on morphology, genetic structure, and abundance of the Sooty-capped Bush Tanager (*Chlorospingus pileatus*), an endemic species restricted to highlands of Costa Rica and western Panama. Abundance and morphology were measured at five study sites and genetic variation was calculated from three microsatellite loci. We expected geographic discontinuities in this species' distribution to have an effect on its morphology and genetic structure. Genetic variation was higher within than between populations with no effect of geographic barriers on population genetic divergence in this species, indicating gene flow is high between populations. Unique alleles were detected in each population and F_{st} values increased with geographic distance between populations. Some morphological traits differed between populations, which may be caused by adaptation to different selective pressures in each population. Molecular data did not differ between the two color morphs that coexist in two isolated populations, which were considered different species. *Received 16 July 2009. Accepted 22 November 2009.*

Highland endemic avian species in the mountains of Costa Rica and western Panama currently show naturally isolated and discontinuous distributions, reflecting their confinement to mountain peaks and their isolation from other highland regions in the Neotropics (Stiles 1983; Barrantes 2000, 2009). Morphological and molecular divergence documented for some of these endemic highland species in Costa Rica correspond to this natural isolation (Stiles 1983, Barrantes 2000, Barrantes and Sánchez 2000). For example, isolated populations of the Volcano Hummingbird (*Selasphorus flammula*) and Fiery-throated Hummingbird (*Panterpe insignis*) differ in coloration and morphological dimensions (Stiles 1983, 1985). Similarly, geographic barriers have affected the genetic and morphological divergence among populations of the Black-and-yellow Phainoptila (*Phainoptila melanoxantha*) (Barrantes 2000, Barrantes and Sánchez 2000).

The Sooty-capped Bush Tanager (*Chlorospingus pileatus*) is endemic to the highlands of Costa Rica and western Panama. This species is naturally restricted to the summit of high mountains and primarily inhabits forest edges and open areas in the cloud forest and páramo. Sooty-capped Bush Tanagers forage in flocks of 5–20 individuals, often accompanied by other small birds (Powell 1985, Stiles and Skutch 1989). A grayish-green morph of Sooty-capped Bush Tanager (lighter morph) coexists on two high volcanoes (Irazú and Turrialba) of central Costa Rica with the darker and more widely distributed morph. The grayish-green morph was first considered a different species (Zeledon's Chlorospingus, *Chlorospingus zeldoni*) by Ridgway (1905), and Eisenmann (1955) and Slud (1964) continued *C. zeledoni* as a different species. However, Carriker (1910) suggested that *C. zeledoni* was a color morph of Sooty-capped Bush Tanager. Johnson and Brush (1972) analyzed the structure and pigment composition of feathers of both taxa and concluded *C. zeledoni* was a morph of Sooty-capped Bush Tanager. However, no further investigations have been conducted to test this hypothesis (e.g., using molecular data).

We used molecular data to analyze the effect of isolation (i.e., distance and barriers between populations) on genetic structure and morphology of the Sooty-capped Bush Tanager. We specifically hypothesized that small populations isolated by effective geographical barriers have a notable reduction in genetic variation. In addition, we searched for genetic differences between the two color morphs on Irazú Volcano. To our knowledge, this is the first fine-scale genetic analysis, using microsatellites of an avian species endemic to the isolated highland regions of Costa Rica and western Panamá. Most species in this hotspot of diversity and endemism are restricted to a reduced portion of the highland forests and have low

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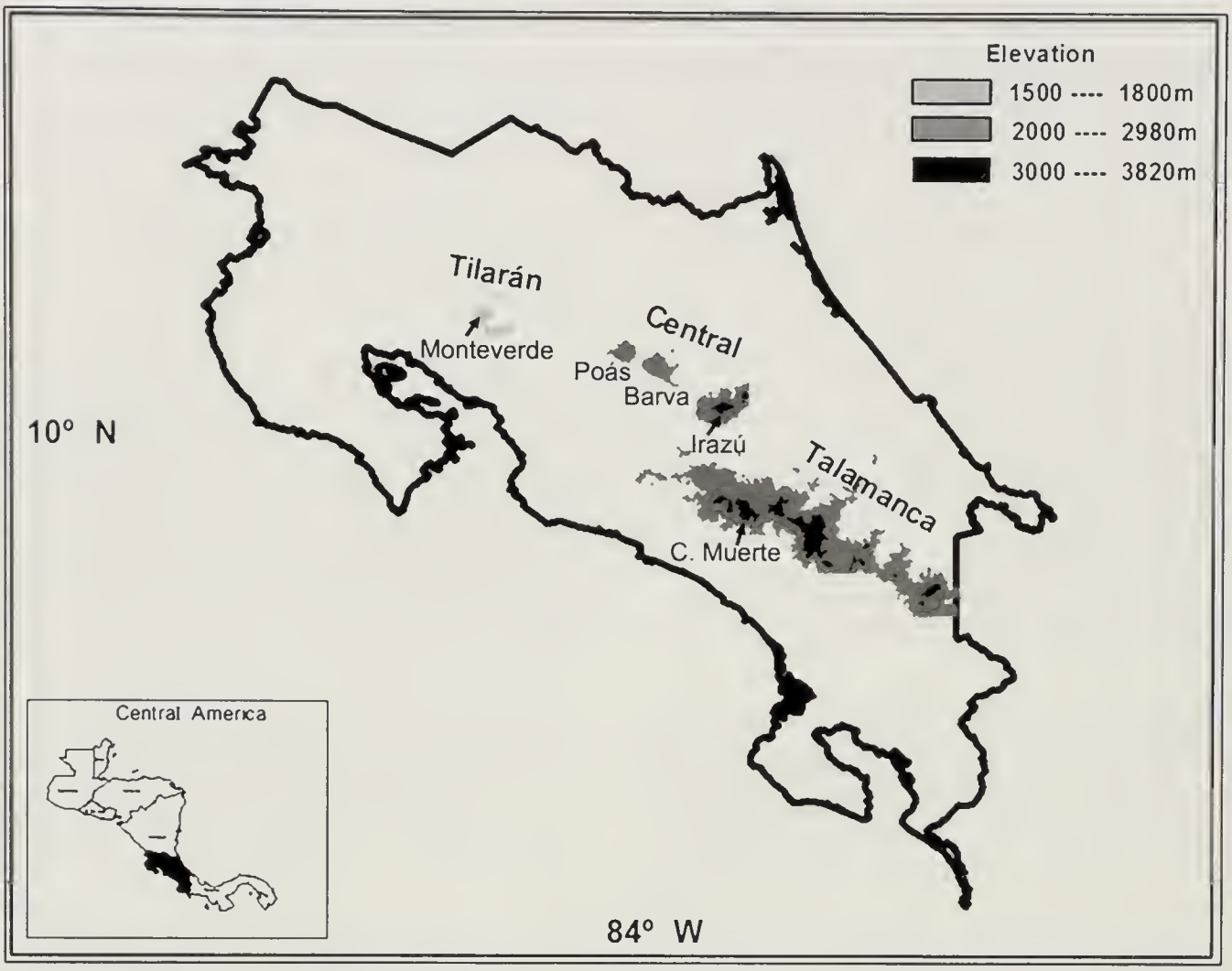

FIG. 1. Sampling localities in Costa Rican mountain ranges: Talamanca, Central Volcanic, and Tilarán. Locations of Monterverde, Irazú, and Cerro de la Muerte are indicated by black arrows.

abundance (Jankowski and Rabenold 2007, Barrantes 2009).

METHODS

Field Data Collection.—We conducted field work in highland forests of three Costa Rican mountain ranges: Talamanca Mountain Range, Central Mountain Range, and Tilarán Mountain Range (Fig. 1) from July 2003 through December 2005. Censuses and tissue collections were conducted at five different sites: Monteverde (10° 19′ N, 84° 47′ W; 1,550 m asl) in the Tilarán Mountain Range; Poás Volcano (10° 11′ N, 84° 13′ W; 2,700 m asl), Irazú Volcano (09° 59′ N, 83° 52′ W; 3,200 m asl), and Barva Volcano (10° 08′ N, 84° 06′ W; 2,800 m asl) in the Central Mountain Range; and Macizo Cerro de la Muerte (09° 33′ N, 83° 43′ W; 3,100 m asl) in the Talamanca Mountain Range. Mountain ranges and field sites within mountain ranges are separated by geographic discontinuities of different magnitude such as watersheds and mountain passes (Fig. 1).

We censused birds 4–7 times in each of the sites to account for possible fluctuations due to climatic conditions. Censuses started at 0545 hrs and all individuals heard and seen within 25 m of each side of the transect were recorded. Length of transects varied from 1.9 to 3.0 km among sites. Thus, abundance was expressed as individuals/km to allow comparison among sites. We used abundance categories based on mean values across censuses for each site. Categories were defined as very common (>20 individuals observed/census), common (10–19 individuals/census), uncommon (5–9 individuals/census), and rare (<5 individuals/census). We calculated the area of the potential available habitat for Sooty-capped Bush Tanagers on each mountain range using Geographical Information Software (ArcView GIS 3.3) on a digital elevation map of Costa Rica (1:200,000; Lambert conformal con-

ical projection) (Fig. 1). This area was estimated from the lower limit of the altitudinal distribution of Sooty-capped Bush Tanager to the summit of the mountains in each mountain range.

We set 5–8 mist nets (12 m long) during each visit to a study site. The following measurements were taken for each individual captured: body mass, length of the beak from distal end of nares to the beak tip, width of the beak at front of nares, length of the culmen from the front of the skull to the beak tip, tarsus from the tibiotarsus joint to the distal end of the tarsometatarsus, flattened wing cord, and tail length. These morphological traits were chosen as they are expected to respond adaptively to ecological differences in habitat (Grant 1986, Price and Boag 1987) and were taken by the same person (GB). Birds were banded (plastic bands) to avoid re-measuring the same individuals. Morphological data were first analyzed using a stepwise (forward) discriminant function analysis (DFA). This option excludes those variables that have no further effect in explaining the between-population variance. We used a MANOVA on those variables included in the DFA. Statistical analyses were performed in Statistica Version 6.0 (StatSoft Inc., Tulsa, OK, USA).

Laboratory Procedures.—DNA was extracted from liver tissue of 56 individuals that had been obtained in previous years and maintained in the tissue collection at the Zoology Museum at the University of Costa Rica. We collected blood samples from five additional individuals for a total of 61 individuals (14 from Cerro de la Muerte, 9 from Irazú Volcano, 18 from Barva Volcano, 11 from Poás Volcano, and 9 from Monteverde). Tissue samples were preserved in 95% alcohol and stored at −20° C until DNA extraction. DNA was extracted using a commercial extraction kit for animal tissue and blood (Promega, Madison, WI, USA) following the specifications provided by the manufacturer.

Genotypes of the 61 individuals were obtained using three microsatellite loci (Escμ1, Escμ4, and Escμ6; Hanotte et al. 1994) isolated from the related species *Emberiza schoeniclus* (Yuri and Mindell 2002). The three microsatellites used were the most polymorphic for *E. schoeniclus*. Microsatellites were amplified using an Eppendorf Mastercycler thermocycler in a volume of 25 μL (12.5 μL of PCR Master Mix 2× PROMEGA, 2.5 μL [10 μm] of each primer, 5 μL of DNA, and 2.5 μL H_2O) following protocols for each locus as described in Hanotte et al. (1994). Genotypes were obtained using an automatic sequencer (ABI Prism 310, Applied Biosystems, Palo Alto, CA, USA). Alleles were sized using program GENOTYPER (3.7NT, Applied Biosystems, Palo Alto, CA, USA).

We counted the number of alleles per locus and calculated their frequencies in each population. We tested deviations of these alleles from Hardy-Weinberg equilibrium with a Chi-square test using program GENALEX 6 (Peakall and Smouse 2006); sequential Bonferroni correction was applied due to performance of multiple simultaneous tests (Rice 1989). The observed (Ho) and expected (He) heterozygosity per locus in each population were calculated using program ARLEQUÍN Version 3.1 (Schneider et al. 2000, Excoffier et al. 2005). An analysis of molecular variance (AMOVA) was used to assess population structure with 30,000 permutations to infer significance of F_{st} values (Weir and Cockerham 1984). AMOVA calculations were conducted using ARLEQUÍN Version 3.1 (http://cmpg.unibe.ch/software/arlequin3). We also checked all loci for the presence of null alleles (Chakraborty et al. 1992, Brookfield 1996) using Micro-Checker Version 2.2.3 (University of Hull, Hull, UK; http://www.microchecker.hull.ac.uk/; van Oosterhout et al. 2004). All loci were tested based on a dinucleotide repeat motif and 1,000 permutations.

We further examined population structure and admixture using a model-based clustering method as implemented in the Bayesian clustering program STRUCTURE (Pritchard et al. 2000, Falush et al. 2003). We inferred population structure using a model which allowed for admixture and correlated allele frequencies. Each Monte Carlo Markov Chain used to infer population structure was based on 1,000,000 iterations and a burn-in of 100,000. Multiple runs were conducted changing the number of putative populations (K) between one and five. At least three independent runs were assessed to estimate the likelihood of the data and the posterior probabilities for each fixed number of populations (K).

We calculated genetic distances between populations using two parameters: Nei's (*Dm*) genetic distance and F_{st} (Nei 1987, Nei and Kumar 2000). We correlated genetic distances (F_{st} values) with geographic distances (km) using a Mantel test and examined whether area of habitat available for

each population correlated with allele number and/or genetic distance (*Dm*) using ARLEQUÍN.

RESULTS

Null Alleles.—We found no evidence of null alleles on the first two loci (Escμ1 and Escμ4) with combined probability for all cases of $P > 0.05$. The third locus (Escμ6) showed a significant homozygote excess congruent with the presence of null alleles ($P < 0.001$). No evidence of scoring errors or allele drop-out was found for any loci. Observed allele frequencies for the third locus only deviated slightly (at 0.01 level) from frequencies estimated considering the presence of null alleles. AMOVA analyses were performed twice using only Escμ1 and Escμ4 loci, and using all three loci. Results were similar with small deviations at the 0.001 level. Thus, we used all three loci for further analysis.

Genetic Variation and Population Structure.—Microsatellite loci were highly polymorphic within each population relative to the number of genotyped individuals (Table 1). Allele number in any locus ranged from seven to 18 across populations. The Barva Volcano population had the highest average number (± SD) of alleles (9.33 ± 0.66), while Monteverde had the lowest (5.67 ± 0.66; Table 2). All populations had unique alleles, although number of these alleles varied across populations: four in Barva, three in Cerro de la Muerte and Monteverde, and two in Irazú and Poás populations (Table 1). Frequency of the allele Escμ6 significantly deviated from Hardy-Weinberg expectations (lower observed values than expected) in Cerro de la Muerte ($X^2 = 64.36$, df = 36, $P = 0.003$), Barva Volcano ($X^2 = 113.56$, df = 45, $P < 0.0001$), and Monteverde ($X^2 = 48.0$, df = 21, $P = 0.001$).

All populations had high levels of genetic diversity based on observed heterozygosity, which did not deviate significantly from expected heterozygosity in all populations (Table 2). Genetic variation was higher within populations than between populations; 98% of the total variance was distributed within populations and only 2% among populations ($\varphi_{st} = 0.0153$; $P > 0.17$). These results are consistent with high levels of gene flow among populations. Genetic structure estimates among populations were similar if the third locus was removed due to the likelihood of null alleles ($\varphi_{st} = 0.0154$; $P > 0.18$). Similarly, analyses using STRUCTURE showed no evidence of significant population structure. The highest likelihood was obtained when the number of populations was set to one (K = 1), which suggests complete admixture.

Pairwise F_{st} values ranged from 0.04 between Barva and Poás to 0.09 between Irazú and Monteverde (Table 3). F_{st} values and geographic distances were not significantly correlated (Mantel test, $r = 0.49$, $P = 0.09$); similar results were obtained using a simple linear correlation.

We did not detect any genotypic difference between three individuals of the grayish-green morph and six individuals of the darker morph in the Irazú population. Both color morphs shared some genotypes.

Morphological Variation.—We captured 72 individual Sooty-capped Bush Tanagers; 24 at Cerro de la Muerte (Estación Biológica Cerro de la Muerte), 11 at Irazú, 18 at Barva, 10 at Poás, and nine at Monteverde. Culmen length, wing cord, tail length, beak width, and body mass differed among populations (DFA: $F_{20,168} = 2.63$, $P = 0.0003$). The Monteverde population had the shortest culmen and wing length and the widest beak; the Irazú population had the longest tail (*Wilks' lambda* = 0.64, df = 16/174, $P = 0.04$; Table 4).

Population Size and Habitat Area.—Sooty-capped Bush Tanagers were very common (>20 individuals/census, corrected by distance) at Barva and Poás, and common at other sites (10–19 individuals/census). The highland habitat available for Sooty-capped Bush Tanagers decreased from the Talamanca Mountain Range to the Tilarán Mountain Range. The Talamanca Mountain Range has 80.8% of the total natural highland habitat potentially available for this species (293,135 ha), while the Central Mountain Range has 17% and the Tilarán Mountain Range has 3%. Area of available habitat was not correlated with number of alleles ($r = 0.53$, $n = 5$, $P = 0.16$) nor with genetic distance (Nei's) ($r = 0.62$, $n = 5$, $P = 0.11$) in Sooty-capped Bush Tanager populations.

DISCUSSION

All populations of the Sooty-capped Bush Tanager had high genetic variation as indicated by genetic diversity indices and number of alleles per locus. The genetic diversity within populations of Sooty-capped Bush Tanager is unexpectedly high for an endemic species with a small and naturally fragmented geographical distribution (Tables 1, 2). Within-population genetic variation

TABLE 1. Allele frequencies for three microsatellite loci (Escμ1, Escμ4, Escμ6) in five populations of Sooty-capped Bush Tanager (n = individuals with amplified microsatellites per loci in each population) in the highlands of Costa Rica.

		Escμ1												Escμ4		
Site	n	132	136	138	142	144	146	148	150	152	154	156	158	n	156	158
C. Muerte	14	0.07	0.14	0.04	0.14	0.00	0.00	0.00	0.11	0.04	0.21	0.00	0.25	14	0.00	0.04
Irazú V.	9	0.00	0.06	0.00	0.22	0.06	0.00	0.06	0.06	0.11	0.00	0.06	0.39	9	0.00	0.06
Barva V.	15	0.00	0.07	0.00	0.03	0.10	0.10	0.00	0.03	0.00	0.27	0.30	0.10	18	0.03	0.00
Poás V.	10	0.00	0.05	0.00	0.25	0.00	0.00	0.00	0.05	0.05	0.05	0.45	0.10	11	0.00	0.00
Monteverde	9	0.00	0.06	0.00	0.00	0.17	0.00	0.00	0.00	0.22	0.39	0.17	0.00	9	0.00	0.00

TABLE 1. Continued.

	Escμ4													Escμ6			
Site	162	164	166	172	174	176	178	180	182	184	186	188	190	n	102	108	110
C. Muerte	0.07	0.00	0.00	0.10	0.21	0.32	0.07	0.07	0.04	0.07	0.00	0.00	0.00	11	0.04	0.00	0.04
Irazú V.	0.00	0.17	0.00	0.16	0.00	0.22	0.06	0.11	0.00	0.06	0.06	0.06	0.00	7	0.00	0.00	0.00
Barva V.	0.00	0.06	0.00	0.14	0.17	0.22	0.11	0.00	0.06	0.06	0.14	0.14	0.06	14	0.04	0.14	0.04
Poás V.	0.00	0.00	0.05	0.30	0.00	0.20	0.05	0.15	0.00	0.00	0.00	0.20	0.00	8	0.00	0.31	0.00
Monteverde	0.00	0.11	0.00	0.29	0.00	0.22	0.22	0.00	0.00	0.00	0.17	0.00	0.00	9	0.00	0.00	0.06

TABLE 1. Continued.

	Escμ6															
Site	112	114	116	118	120	122	124	126	128	134	136	n	146	148	156	160
C. Muerte	0.00	0.00	0.27	0.04	0.00	0.04	0.18	0.23	0.04	0.00	0.00	11	0.00	0.00	0.09	0.00
Irazú V.	0.00	0.06	0.07	0.43	0.07	0.00	0.14	0.14	0.07	0.00	0.00	7	0.00	0.00	0.00	0.00
Barva V.	0.00	0.10	0.00	0.11	0.00	0.29	0.07	0.07	0.04	0.00	0.04	14	0.21	0.04	0.00	0.00
Poás V.	0.00	0.00	0.06	0.12	0.06	0.12	0.06	0.06	0.00	0.00	0.00	8	0.00	0.06	0.12	0.00
Monteverde	0.06	0.17	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.06	0.00	7	0.00	0.00	0.00	0.12

TABLE 2. Number of individuals (*n*), allele number (Na), observed heterozygosity (Ho), and expected heterozygosity (He) calculated for each locus in five populations of Sooty-capped Bush Tanager in Costa Rica.

	Escμ1				Escμ4				Escμ6				Totals (mean ± SD)			
	n	Na	Ho	He	*n*	Na	Ho	He	*n*	Na	Ho	He	*n*	Na	Ho	He
C. Muerte	14	8	0.77	0.68	14	9	0.71	0.85	11	9	0.45	0.86	13.0 ± 1.73	8.67 ± 0.33	0.65 ± 0.14	0.86 ± 0.07
Irazú V.	9	8	0.78	0.81	9	10	0.89	0.91	7	7	0.50	0.81	8.33 ± 1.15	8.83 ± 0.88	0.75 ± 0.13	0.85 ± 0.05
Barva V.	15	8	0.87	0.82	18	10	0.67	0.83	14	10	0.21	0.86	15.66 ± 2.08	9.33 ± 0.66	0.78 ± 0.27	0.86 ± 0.02
Poás V.	10	8	0.70	0.77	11	7	0.90	0.84	8	8	0.62	0.83	9.33 ± 1.15	7.67 ± 0.33	0.74 ± 0.12	0.83 ± 0.04
Monteverde	9	8	0.78	0.81	9	10	0.89	0.91	7	7	0.50	0.81	8.66 ± 0.57	5.67 ± 0.66	0.60 ± 0.25	0.74 ± 0.03

is expected to be small compared to between-population variation in species with small ranges and fragmented distributions, mainly due to genetic drift or founder effects and small effective population size (Peterson et al. 1992, Avise 1994). The absence of genetic structure among populations of Sooty-capped Bush Tanagers indicates gene flow may be relatively high among populations, counteracting the effects of genetic drift, small effective population size, and local adaptation even in small populations (Avise 1994). However, time since population isolation may have also affected the near absence of genetic structure in this endemic species. Populations are expected to retain most of their original genetic composition (Templeton et al. 1995) if isolation is relatively recent, as it has been hypothesized for Costa Rican highland endemic species (Stiles 1983, Barrantes and Sánchez 2000, Weir 2006, Barrantes 2009),

There were some genetic and morphological differences across populations of the Sooty-capped Bush Tanager. For example, the presence of unique alleles in each population indicates that processes of random drift, inbreeding, and perhaps local adaptation are causing the genetic differences among populations. Genetic difference between populations (F_{st} values) tend to increase with geographic distance ($P = 0.09$) suggesting some limitation in dispersal. However, gene flow among populations likely dilutes the effect of these processes. Schwartz et al. (1986) indicated that gene flow rates as low as one migrant per generation are generally effective to prevent loss of genetic variation from habitat fragmentation.

Morphology differed among some Sooty-capped Bush Tanager populations. Morphological differences may be caused by different abiotic and biotic pressures operating on different populations. For example, the habitat of the Sooty-capped Bush Tanager in Monteverde is exposed to relatively intense trade winds year round (Clark et al. 2000). Birds in this population had shorter wings (Table 4), which are more efficient at maneuvering under strong wind conditions (Pennycuick 1968, Thomas 1996, Marguerie et al. 2007). There is no clear explanation for differences in other morphological traits (e.g., culmen, tail, and beak width), as fruit species and habitat structure appear similar across localities (Barrantes and Loiselle 2002). Morphological divergence between populations has been reported for other endemic birds in the highlands of Costa Rica

TABLE 3. Geographic distance (km) (above diagonal) and F_{st} values (below the diagonal) between five populations of Sooty-capped Bush Tanager in the highlands of Costa Rica.

Site	C. Muerte	Irazú V.	Barva V.	Poás V.	Monteverde
C. Muerte	—	47	74	91	142
Irazú V.	0.042	—	34	48	103
Barva V.	0.047	0.063	—	15	71
Poás V.	0.063	0.060	0.040	—	55
Monteverde	0.053	0.090	0.059	0.078	—

(Stiles 1983, 1985; Barrantes and Sánchez 2000), indicating rapid morphological divergence among populations, if recent population fragmentation is assumed (Stiles 1983, 1985; Barrantes and Sánchez 2000; Barrantes 2009). The lack of concordance between morphology and genetics in this study is possibly caused, at least in part, by the intrinsic characteristics of the microsatellites. These genetic markers are neutral (or nearly so) whereas morphological traits are frequently under strong selective pressures (Zwartjes 2003, Santiago-Alarcon et al. 2006), and changes in traits presumed to be under selection often do not correlate with variation of microsatellites (Phillimore et al. 2008) or mitochondrial DNA markers (McCormack et al. 2008, Weir et al. 2008).

We found no genetic differences between the two color morphs in the Irazú population. Genotypes vary among individuals of each morph and some genotypes are shared with individuals of the other morph. Our findings support the hypothesis of Carriker (1910) and Johnson and Brush (1972), who suggested that differences in coloration reflect two morphs of the same species. We found individuals of the grayish-green morph vary greatly in coloration. All grayish-green birds also had yellow nasal tufts, and one had one yellow secondary feather in its right wing (GB, unpubl. data). Evidence that helps explain this polymorphism is elusive. Birds of both morphs use the same habitat, forage together, and apparently mate with each other (Johnson and Brush 1972; GB, unpubl. data). Johnson and Brush (1972) suggested that brighter coloration of grayish-green individuals is favored during periods of high volcanic activity when ash in the atmosphere reduces visibility. However, information on abundance of each morph during high and low volcanic activity periods is needed to test this hypothesis. This polymorphism may have evolved recently by assortative mating with some reproductive barriers, but its detection only would be possible with detailed genetic and behavior studies (Yeh 2004, McGlothlin et al. 2005).

The geographic distribution of the Sooty-capped Bush Tanager on only three mountain ranges, the number of naturally isolated populations ($n = 5$), as well as the low number of alleles analyzed ($n = 3$) imposed some restrictions on analyses and limited the statistical power of some results. For example, the low number of microsatellite loci limited use of more detailed analyses to quantify gene flow. Similarly, lack of significant correlation between geographic and pairwise genetic differences was likely caused by the small number of isolated populations. In addition, we did not survey Sooty-capped Bush Tanagers in western Panamá where the Fortuna Mountain Pass may limit bird movement across this geographic discontinuity, affecting the scope of our findings.

The geographic discontinuities that separate populations of Sooty-capped Bush Tanagers as well as the area of available habitat appear to have had little effect in shaping the genetic structure of this endemic species. The presence of divergent morphologies and color morphs in some populations and unique alleles in all populations of Sooty-capped Bush Tanager suggest some isolation and/or local adaptation of populations (Stiles 1983, 1985; Barrantes and Sánchez 2000). This

TABLE 4. Morphologieal traits (mean ± SD) for five populations of Sooty-eapped Bush Tanager in the highlands of Costa Riea. (Length = mm, body mass = g).

	Morphology traits						
Site	Culmen length	Wing cord	Tail length	Tarsus length	Beak length	Beak width	Mass
C. Muerte	15.35 ± 1.11	71.6 ± 2.91	64.0 ± 4.65	23.85 ± 0.76	6.38 ± 0.32	6.38 ± 0.32	19.90 ± 1.44
Irazú V.	16.0 ± 0.84	70.31 ± 2.63	55.0 ± 2.20	24.21 ± 0.88	6.41 ± 0.28	6.42 ± 0.28	19.87 ± 0.87
Barva V.	15.22 ± 0.91	69.7 ± 2.70	61.66 ± 3.52	23.70 ± 0.76	6.40 ± 0.48	6.40 ± 0.48	20.28 ± 1.16
Poás V.	15.88 ± 1.15	69.5 ± 2.51	61.93 ± 2.09	23.68 ± 0.90	6.36 ± 0.38	6.36 ± 0.38	20.37 ± 2.57
Monteverde	13.58 ± 2.71	68.1 ± 4.35	55.57 ± 3.69	23.14 ± 1.15	6.43 ± 0.77	6.43 ± 0.77	17.65 ± 1.67

system of geographically isolated populations deserves special conservation attention, because it presents a unique opportunity to further study incipient causes of population divergence in an area of high endemism.

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LONG-TERM CHANGES IN AVIAN COMMUNITY STRUCTURE IN A SUCCESSIONAL, FORESTED, AND MANAGED PLOT IN A REFORESTING LANDSCAPE

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ABSTRACT.—We examined a 35-year transition in the breeding bird community at a successional study site in a reforesting landscape in southwestern New York, USA. Changes in the successional plot were compared with those in two additional census plots, one in undisturbed forest and the other in a managed tree farm. The territories of 7,429 singing male songbirds were mapped on the census plots. The most dramatic changes in community structure were in the successional plot where total number of territories declined between the beginning of the study ($\bar{x}$ = 95.8 territories, 1969–1973) and end of the study ($\bar{x}$ = 57.2 territories, 1999–2003); grassland/shrub nesting species were nearly extirpated, and the number of neotropical migrant territories increased from zero in 1969 to 30 in 2003. The average number of neotropical migrant territories in the undisturbed forest plot declined from the beginning of the study ($\bar{x}$ = 54.0, 1975–1979) to the end ($\bar{x}$ = 44.8, 2003–2007). The average number of territories increased in the managed tree farm from the beginning of the study ($\bar{x}$ = 53.6, 1983–1987) to the end ($\bar{x}$ = 104.0, 2003–2007) largely due to increases in abundance of temperate zone migrants and resident species. Counts of individual species in the census plots were not highly correlated with counts from regional Breeding Bird Survey routes. *Received 28 March 2009. Accepted 20 October 2009.*

Long-term studies are required to better understand the effects of anthropogenic change on natural ecosystems (Collins 2001), and a need for detailed long-term studies in ornithology has been recognized (Wiens 1984). Relatively few studies follow populations for more than two decades; many long-term studies have not followed the same protocol every year (Hall 1984, Leck et al. 1988, McNulty et al. 2008), or have only sampled avian communities at end points of a long time period (Ambuel and Temple 1982, Kirk et al. 1997, Haney et al. 2008). Studies examining changes in community structure following anthropogenic or natural change have tended to focus on succession following timber harvests or forest fires (Hagan et al. 1997, Hobson and Schieck 1999, Venier and Pearce 2005).

Recent attention has focused on the influence of forest fragmentation on bird communities (Stephens et al. 2004), but many areas are undergoing large-scale regeneration rather than forest fragmentation. Little attention has been directed at avian community structure following agricultural abandonment and secondary succession (but see Johnston and Odum 1956), a widespread process in eastern North America. Many areas in New England support more forested land today than at any point in the last two centuries as marginal agricultural lands are abandoned and allowed to undergo secondary succession, resulting in profound changes in bird communities (Hagan 1993). Grassland bird declines have been attributed, in part, to abandonment and reforestation of farmland (Norment 2002); the grassland area in New York and New England has declined by 60% since the 1930s (Vickery et al. 1994). Secondary succession and maturation of forests have been cited as mechanisms driving long-term changes in populations of shrub specialists like the Eastern Towhee (*Pipilo erythrophthalmus*) (Hagan 1993) and species that prefer early-successional forest like the Least Flycatcher (*Empidonax minimus*) (Holmes and Sherry 1988). Additional studies of avian community changes during and following agricultural abandonment are warranted, and would benefit from long-term studies at focal sites.

Intensive, long-term field studies can also be useful for assessing and validating the utility of larger-scale monitoring data. For instance, results from intensive studies have been compared with regional trends detected by the Breeding Bird Survey (BBS) (Holmes and Sherry 2001, Ballard et al. 2003, McNulty et al. 2008). These local, intensive studies may not be subject to many of the limitations often associated with BBS data such as road-bias or changes in observers (Kendall et al. 1996, Keller and Scallan 1999, Niemuth et al. 2007). We can have greater confidence in the results if trend estimates generated from different methodologies agree.

We document a 35-year transition in the breeding bird community at a study site that has

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undergone secondary succession in a region experiencing reforestation. In addition, we compare trends on the successional plot with additional long-term censuses of a forested plot and on an actively managed tree farm. Our objectives were to: (1) quantify long-term changes in breeding bird communities on intensively studied plots that experienced different management regimes, and (2) compare changes in the avian communities on the census plots with regional trends measured by the Breeding Bird Survey.

METHODS

Intensive Census Plots.—Breeding bird territories were mapped on three long-term census plots. Territories were defined by spot mapping (Svenson et al. 1970), a reliable method of estimating populations of breeding birds (James and Wamer 1982). At least eight visits were made to each plot at approximately weekly intervals during the breeding season from late May to late July annually. All observations were recorded by a single observer (EWB) throughout the course of the study. The census plots were searched during each visit on foot for ~1.5 hrs, and territories of singing males were mapped. All partial territories (territories extending beyond the boundaries of the study plots) were considered to be whole territories in the analysis.

A 9.3-ha "successional" plot transitioned from an open agricultural field to secondary growth forest during the study (35 years, 1969–2003). The "forest" plot was a 16.6-ha area in mixed deciduous-coniferous forest that was relatively undisturbed during the course of the study (33 years, 1975–2007). The "plantation" plot included 10.7 ha in an actively managed Christmas tree farm; the habitat was maintained at a relatively early successional stage in the plantation plot, although vegetation height increased over the course of the study (25 years, 1983–2007). All three plots were in Allegany County (42° 14′ N, 77° 49′ W) in southwestern New York State.

BBS Trends.—The Breeding Bird Survey (BBS) is an annual survey of bird diversity and abundance conducted along hundreds of roadside routes in North America during the breeding season each year. A route is composed of a series of 50 stops distributed across 39.4 km. A skilled volunteer observer records all individual birds that are heard or observed at each stop during a 3-min point count (Robbins et al. 1986). Data from the two BBS survey routes nearest to the census plots were analyzed for this study (routes 61045 and 61046). These BBS routes were surveyed by the same observer as the census plots (EWB) with the observer being the primary recorder on these routes beginning in 1991 (route 61045) and 1973 (route 61046).

Data Analysis.—Population trends for each species on each census plot were calculated with Poisson regression using Proc GENMOD in SAS (SAS Institute 2003). Poisson models adequately fit the data in 137 of 141 runs (using the Deviance Chi-square method; models not fitting the data showed signs of overdispersion). Species were included in the analysis if they were detected in at least 5 years within a plot. Data from Tree Swallows (*Tachycineta bicolor*) and Eastern Bluebirds (*Sialia sialis*) were eliminated from analysis as the presence of these species was dependent upon the availability of artificial nesting boxes, and nest boxes were not consistently provided throughout the course of the study.

Birds were grouped according to life history characteristics (Table 1) and species were classified by migration strategy (neotropical migrant vs. temperate migrant/resident) and by preferred breeding habitat (woodland vs. grassland/shrub). Classifications were based on life history information available through the Patuxent Wildlife Research Center (Gough et al. 1998). Species richness was calculated within years as the total number of species detected on the plot.

Counts for BBS routes 61045 and 61046 were downloaded from the BBS web site (Sauer et al. 2008). We tested for correlations between BBS counts and census counts for all years with census data except for 2006 when the BBS was not conducted on route 61046. Correlations coefficients (r) among counts over time for all census plot/BBS route combinations were calculated using Proc CORR in SAS.

RESULTS

Widespread changes in the avian community were detected on the successional plot where number of total territories declined ($\chi^2_1 = 138.8$, $P < 0.001$) and grassland-nesting species essentially disappeared. Numerous nesting species were lost from the plot within the first 10 years including Clay-colored Sparrow (*Spizella pallida*), Vesper Sparrow (*Pooecetes gramineus*), Savannah Sparrow (*Passerculus sandwichensis*), Henslow's

TABLE 1. Species, life-history classifications, number of territories recorded, and trend estimates for breeding birds recorded on long-term studies conducted in successional, forest, and tree farm (plantation) census plots.

Species		Breeding habitat[a]	Migration status[b]	Successional *n* (trend)[c]	Forest *n* (trend)	Plantation *n* (trend)
Ruffed Grouse	*Bonasa umbellus*	W	T	19 (+)	6	.
Wild Turkey	*Meleagris gallopavo*	W	T	.	11	.
Sharp-shinned Hawk	*Accipiter striatus*	W	T	.	5	.
Cooper's Hawk	*A. cooperii*	W	T	.	5	.
Red-shouldered Hawk	*Buteo lineatus*	W	T	.	10 (+)	.
Broad-winged Hawk	*B. platypterus*	W	N	.	24	.
Mourning Dove	*Zenaida macroura*	S	T	18 (+)	6	23 (+)
Black-billed Cuckoo	*Coccyzus erythopthalmus*	W	N	10 (−)	.	.
Barred Owl	*Strix varia*	W	T	.	12	.
Yellow-bellied Sapsucker	*Sphyrapicus varius*	W	T	.	9 (+)	.
Downy Woodpecker	*Picoides pubescens*	W	T	.	16	.
Hairy Woodpecker	*P. villosus*	W	T	.	17	.
Pileated Woodpecker	*Dryocopus pileatus*	W	T	.	7	.
Alder Flycatcher	*Empidonax alnorum*	S	N	41	.	.
Great Crested Flycatcher	*Myiarchus crinitus*	W	N	.	10 (+)	.
Eastern Kingbird	*Tyrannus tyrannus*	S	N	9	.	13
Blue-headed Vireo	*Vireo solitarius*	W	N	11 (+)	81 (+)	.
Red-eyed Vireo	*V. olivaceus*	W	N	.	8	.
Blue Jay	*Cyanocitta cristata*	S	T	33 (+)	91	7 (+)
American Crow	*Corvus brachyrhynchos*	N/A	T	.	19 (+)	.
Horned Lark	*Eremophila alpestris*	S	T	.	.	8
Black-capped Chickadee	*Poecile atricapillus*	W	T	32 (+)	112	.
Red-breasted Nuthatch	*Sitta canadensis*	W	T	8 (+)	94	.
White-breasted Nuthatch	*S. carolinensis*	W	T	.	11 (−)	.
Brown Creeper	*Certhia americana*	W	T	.	68	.
House Wren	*Troglodytes aedon*	S	N	.	25	.
Winter Wren	*T. troglodytes*	W	T	.	17 (+)	.
Golden-crowned Kinglet	*Regulus satrapa*	W	T	17 (+)	209	.
Veery	*Catharus fuscescens*	W	N	.	22 (−)	.
Hermit Thrush	*C. guttatus*	W	T	.	18 (+)	.
Wood Thrush	*Hylocichla mustelina*	W	N	.	44 (−)	.
American Robin	*Turdus migratorius*	S	T	176 (−)	98	102 (+)
Gray Catbird	*Dumetella carolinensis*	S	N	30	.	9
Brown Thrasher	*Toxostoma rufum*	S	T	14 (−)	.	17
Cedar Waxwing	*Bombycilla cedrorum*	S	T	102 (+)	20 (+)	136 (+)
Blue-winged Warbler	*Vermivora pinus*	S	N	8 (+)	.	.
Nashville Warbler	*V. ruficapilla*	S	N	26	.	.
Chestnut-sided Warbler	*Dendroica pensylvanica*	S	N	17 (+)	26 (+)	.
Magnolia Warbler	*D. magnolia*	W	N	78 (+)	308	15 (+)
Yellow-rumped Warbler	*D. coronata*	W	T	105 (+)	128 (+)	70 (+)
Black-throated Green Warbler	*D. virens*	W	N	12	337 (−)	.
Blackburnian Warbler	*D. fusca*	W	N	10 (+)	323	.
Prairie Warbler	*D. discolor*	S	N	7	.	24
Ovenbird	*Seiurus aurocapilla*	W	N	18 (+)	77	.
Mourning Warbler	*Oporornis philadelphia*	S	N	.	19 (+)	.
Common Yellowthroat	*Geothlypis trichas*	S	N	195	82	22
Canada Warbler	*Wilsonia canadensis*	W	N	.	8 (−)	.
Scarlet Tanager	*Piranga olivacea*	W	N	.	18 (−)	.
Eastern Towhee	*Pipilo erythrophthalmus*	S	T	82 (−)	.	29
Chipping Sparrow	*Spizella passerina*	S	T	375 (−)	69	430 (+)
Field Sparrow	*S. pusilla*	S	T	129 (−)	.	102 (−)
Vesper Sparrow	*Pooecetes gramineus*	S	T	.	.	15
Savannah Sparrow	*Passerculus sandwichensis*	S	T	.	.	45 (−)
Grasshopper Sparrow	*Ammodramus savannarum*	S	N	.	.	26 (−)
Song Sparrow	*Melospiza melodia*	S	T	414 (−)	39	378 (+)

TABLE 1. Continued.

Species		Breeding habitat[a]	Migration status[b]	Successional *n* (trend)[c]	Forest *n* (trend)	Plantation *n* (trend)
White-throated Sparrow	*Zonotrichia albicollis*	S	T	18 (+)	17	.
Dark-eyed Junco	*Junco hyemalis*	W	T	40 (+)	246	.
Northern Cardinal	*Cardinalis cardinalis*	S	T	6	9 (−)	.
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	W	N	.	9 (−)	.
Indigo Bunting	*Passerina cyanea*	S	N	60 (+)	51	22
Bobolink	*Dolichonyx oryzivorus*	S	N	.	.	31
Red-winged Blackbird	*Agelaius phoeniceus*	S	T	.	.	30
Brown-headed Cowbird	*Molothrus ater*	S	T	52 (−)	34	19 (+)
Purple Finch	*Carpodacus purpureus*	W	T	114 (−)	56 (+)	83 (+)
House Finch	*C. mexicanus*	N/A	T	.	.	7
American Goldfinch	*Spinus tristis*	S	T	6	.	50 (+)

[a] Breeding habitat and migration classifications are from Gough et al. (1998), W = woodland nesting species, S = successional species including grassland and shrubland nesting birds.

[b] T = temperate, including permanent residents and short-distance migrant species, N = neotropical migrants.

[c] Trend sign indicates significant ($P < 0.05$) population increase (+) or decrease (−) over time, and period (.) = insufficient data. No sign indicates the lack of a significant directional trend.

Sparrow (*Ammodramus henslowii*), Bobolink (*Dolichonyx oryzivorus*), Red-winged Blackbird (*Agelaius phoeniceus*), and Common Grackle (*Quiscalus quiscula*). The number of territories of neotropical migrants ($\chi^2_1 = 50.5$, $P < 0.001$) and woodland-nesting species ($\chi^2_1 = 55.1$, $P < 0.001$) increased despite the decline in total territories on the successional plot, (Fig. 1A). Positive trends were detected for 17 species (49%, $P < 0.05$, Table 1) and declines were detected for nine species (26%). Total species richness varied considerably but increased over time ($\chi^2_1 = 23.2$, $P < 0.001$, Fig. 2).

The avian community on the forest plot remained relatively stable with significant declines detected for eight species (17%, Table 1) and increases detected for 12 species (25%). No trends were detected in total territories ($\chi^2_1 = 0.1$, $P = 0.712$) or in species richness ($\chi^2_1 = 0.6$, $P = 0.430$) over time. The number of territories of neotropical migrants declined ($\chi^2_1 = 9.2$, $P = 0.003$) while territories of shorter-distance migrants and resident species increased ($\chi^2_1 = 12.6$, $P < 0.001$, Fig. 1B).

The total number of territories increased on the managed tree farm ($\chi^2_1 = 101.9$, $P < 0.001$), where the number of breeding pairs significantly increased for 11 species (42%, Table 1) and declined for only three species (12%). Increases in number of territories were primarily among resident and temperate-zone migrants ($\chi^2_1 = 52.1$, $P < 0.001$) with grassland/shrub nesting species ($\chi^2_1 = 20.8$, $P < 0.001$) and woodland nesting species ($\chi^2_1 = 55.8$, $P < 0.001$) becoming more common over time (Fig 1C).

Counts of species on local BBS routes were not highly correlated with counts of breeding territories for each species on the census plots. Comparing counts on BBS route 61045 with the census plots, the average correlation coefficients were greatest for the successional plot ($\bar{x}$ correlation, $r = 0.25$), followed by the managed tree farm ($\bar{x} = 0.14$) and forest plot ($\bar{x} = 0.07$). Counts of individual species on BBS route 61046 were also best correlated with counts on the successional plot ($\bar{x} = 0.23$), followed by the forest plot ($\bar{x} = 0.16$) and plantation plot ($\bar{x} = -0.06$). On average, the counts of individual species on the two BBS routes were not highly correlated ($\bar{x} = 0.17$).

DISCUSSION

We documented profound changes in community structure and abundance of birds in an area undergoing secondary succession following agricultural abandonment, while a nearby, undisturbed forest bird community remained relatively static. The importance of disturbance and succession in structuring avian communities has long been appreciated despite the paucity of long-term studies documenting the dynamic changes in communities over time (reviewed by Brawn et al. 2001). Some form of disturbance is required to meet the habitat needs of many species, and the loss of grassland and shrub habitats in North America has contributed to great declines in birds

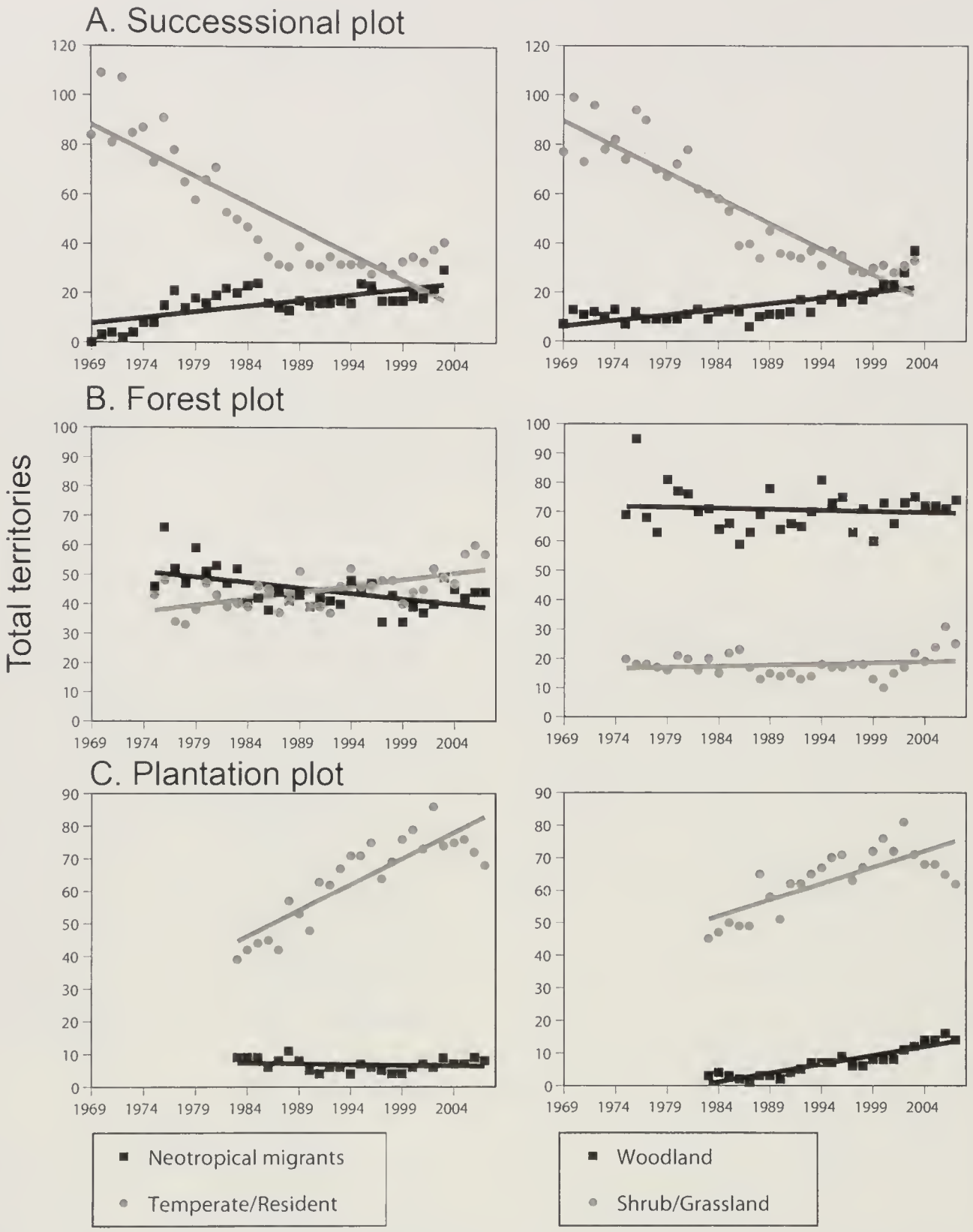

FIG. 1. Total territories (n = 7,429) mapped on intensive census plots over 35 years, where temperate migrants and resident species that nest in early successional habitats demonstrated the strongest trends, declining in the successional landscape (A), remaining relatively stable in an undisturbed forest plot (B), and becoming more common in the managed tree farm (plantation, C).

that specialize in these environments (Askins 2000, Brawn et al. 2001).

Clearing of forests in eastern North America created early-successional habitats that allowed for geographic spread and numerical increases of species adapted to these environments. Recent changes in land use patterns, however, have led to a dramatic shift in the structure of bird communities. The area of cultivated cropland east of the Mississippi River declined by ~22% between 1950 and 2000 (Brown et al. 2005), largely due to the loss of small farms. These declines in small-

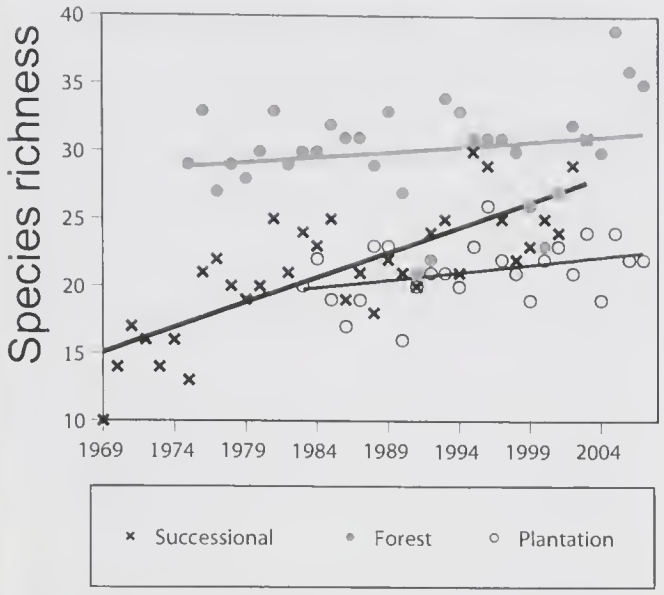

FIG. 2. Changes in species richness on census plots in successional, forested, and managed tree farm (plantation) habitats.

scale agriculture contributed to similar declines in populations and distributions of early-successional birds, leading to local and regional extirpation of some species (Hunter et al. 2001).

Johnston and Odum (1956) documented changes in the richness of species nesting in the Piedmont of Georgia on plots of various successional stages with increasing richness recorded with increasing age of the vegetation. We also found an increase in species richness during the early stages of secondary succession. However, in contrast to the earlier study, density of nesting birds decreased significantly as our successional study site transitioned from grassland to forest over a 35-year period. The rapid decline in grassland- and shrub-nesting species was not matched by a similarly rapid increase in woodland-nesting birds, many of which are neotropical migrants.

This lack of replacement by woodland-nesting species may be a function of a general decline in the abundance of neotropical migrants in the region (Robbins et al. 1989). Holmes and Sherry (2001), in one of the few intensive, long-term studies of breeding bird communities, recorded a decline in the abundance of breeding birds in a 30-year study in relatively undisturbed, contiguous forest in New Hampshire. Declines were most pronounced for neotropical migrants. Other studies have reported long-term declines in populations of long-distance migrants at sites in West Virginia (Hall 1984), New Jersey (Leck et al. 1988), and Sweden (Enemar et al. 1994). In contrast, Askins and Philbrick (1987) detected a decline and subsequent rebound in abundance of many neotropical migrants during a 32-year study at an isolated 23-ha woodlot in Connecticut. The amount of forest in the surrounding landscape during the Connecticut study initially declined and then increased, suggesting a link between abundance of long-distance migrants and regional forest area.

A general decline in abundance of long-distance migrants could explain the relatively shallow increase in neotropical migrant territories on our successional study plot as the habitat became more suitable for many of these woodland-breeding birds. As in the earlier studies, the abundance of long-distance migrants declined over time on the undisturbed forest plot censused in our study, suggesting that local populations of neotropical migrants may be declining.

Quantifying changes in the abundance and distribution of birds remains one of the major methodological challenges in avian ecology and conservation biology. Most population and trend estimates in North America are based on Breeding Bird Survey data, yet concerns over the adequacy of the BBS continue to be raised (Keller and Scallan 1999, Francis et al. 2005) and addressed through novel analytical techniques (e.g., Royle et al. 2005). Confidence in trend estimates generated from BBS data can be strengthened if these trends agree with data from other monitoring schemes. For instance, McNulty et al. (2008) compared long-term trends in an old-growth forest plot with regional BBS trends in a relatively static landscape (the Adirondack Mountains of New York) and found agreement in the direction of the trend for 74% of the species monitored. Our comparison of bird counts on local BBS routes with counts on intensive census plots failed to show high agreement among the surveys. The greatest agreement, however, was between the BBS routes and the successional plot, a logical result in a region experiencing the abandonment of small-scale agriculture.

Analyses comparing results of long-term, intensive research with broad-scale monitoring programs such as the BBS should provide a more complete picture of the status of and temporal changes in bird populations. Intensive studies may be the only way to monitor trends in abundance and distribution of species that are hard to detect, or species that occur in low densities. For example, Clay-colored Sparrows were not detect-

ed on either BBS route in the current study, although they were recorded nesting within the successional and managed tree farm plots.

Long-term, intensive studies can provide unique perspectives on ecological phenomena that are unattainable in most contemporary studies that occur over restricted temporal scales. More long-term research projects should be encouraged (Wiens 1984). Further, fluctuations in populations detected in this study and elsewhere (Holmes and Sherry 2001) highlight the value and necessity of conducting continuous, long-term studies when studying population trends.

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SCALE-DEPENDENT RESPONSE BY BREEDING SONGBIRDS TO RESIDENTIAL DEVELOPMENT ALONG LAKE SUPERIOR

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ABSTRACT.—We examined the influence of shoreline residential development on breeding bird communities along forested portions of Lake Superior and hypothesized that anthropogenic changes related to housing development would alter bird community structure compared to areas without human development. We used point counts to compare relative abundance of bird species in relation to residential development at coarse (along 1 km shoreline stretches with and without housing/cottage development) and fine (developed and undeveloped sides of a shoreline access road) spatial scales during the 2005 breeding season. More species had development related differences in abundance at the finer-scale analysis than at the coarse scale. American Crows (*Corvus brachyrhynchos*) and American Robins (*Turdus migratorius*) were more abundant on the developed, shoreline side of shoreline access roads. Red-breasted Nuthatches (*Sitta canadensis*), Black-throated Green Warblers (*Dendroica virens*), and Red-eyed Vireos (*Vireo olivaceus*) were more abundant on the undeveloped, inland side of shoreline access roads. Several species were detected exclusively in developed or undeveloped forest areas. The pattern of development-related differences in relative abundance of bird species depended on the scale at which data were analyzed, suggesting that many species may respond to habitat differences within the 100 m scale quite distinct from how they respond to differences at the scale of thousands of meters. *Received 27 August 2009. Accepted 23 December 2009.*

Rural population growth in many parts of the United States has increased in the last 15 years (Long and Nucci 1997, Gustafson et al. 2005). Growth in parts of the northern Great Lakes Region has been concentrated around inland lakes (Radeloff et al. 2001, Gonzalez-Abraham et al. 2006). Two-thirds of previously undeveloped inland lakes in northern Wisconsin (i.e., lakes with no residential housing) have become developed with homes and cottages near the shoreline since 1965 (Lindsay et al. 2002, Elias and Meyer 2003). Housing development alters shoreline habitat through changes in habitat structure and plant species composition, which can create discontinuities in plant communities resulting in fragmentation (Brown 2003). These changes have the potential to influence many taxa including forest birds (Vale and Vale 1976, Mills et al. 1989, Theobald et al. 1997, Swenson and Franklin 2000).

Many recent studies focusing on the ecological impacts of nearshore residential development have examined inland lakes with less attention on Great Lakes shorelines (Rottenborn 1999, Lindsay et al. 2002, Elias and Meyer 2003). Perimeters of both inland lakes and the Great Lakes provide an interface between aquatic and upland ecosystems but, because of their size and associated climatological influence, the abiotic and biotic environment along Great Lakes shorelines often differs dramatically from inland lake riparian zones or adjoining upland habitats (Eichenlaub 1979, Albert et al. 1986). Thus, results from studies of inland lakes cannot be confidently extended to larger lake systems.

North America's Great Lakes (Huron, Ontario, Michigan, Erie, and Superior) contain 20% of the world's and 95% of North America's surface fresh water. The waters of the Great Lakes support the world's largest freshwater commercial fishery, supply drinking water to millions of citizens in the United States and Canada, and support a multi-million dollar recreation industry (Great Lakes Information Network 2005). The amenity values associated with the 17,542 km of Great Lakes shoreline have likewise attracted residential development (Schnaiberg et al. 2002). Shoreline residential development on the Great Lakes has accelerated in recent years and now represents one of the fastest growing segments of rural housing expansion in the region (Orr 1997).

The Keweenaw Peninsula is in the western Upper Peninsula of Michigan and is surrounded on three sides by Lake Superior (Fig. 1). Keweenaw County is one of the least populated in Michigan and much of the shoreline remains undeveloped; however, residential development in this area has rapidly increased over the past decade with population shifts to rural areas (Orr 1997). The Upper Peninsula has not yet felt the

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effects of rural in-migration as greatly as other scenic places in the United States, but land use changes and population increases are evident (Orr 1997).

We focused on differences between residentially developed and undeveloped shoreline areas of Lake Superior and measured vegetation habitat features associated with development known to influence bird presence and relative abundance. To our knowledge, this is the first study to examine the influence of Great Lakes shoreline residential development on forest breeding bird communities on any of the Great Lakes. Our objectives were to: (1) evaluate differences in forest vegetation between developed and undeveloped areas, (2) examine if relative abundance of breeding bird species differs between residentially developed and undeveloped shoreline forest along Lake Superior, and (3) assess the spatial scale at which development influences bird presence and abundance.

METHODS

Study Sites.—The study was conducted in two residentially developed and three undeveloped shoreline areas along the eastern shore of Lake Superior in the Keweenaw Peninsula in the northern-most part of the Michigan's Upper Peninsula (Fig. 1). Only east and southeast facing areas were used to minimize variability in soils, bedrock geology, site aspect, wind, and forest type. Developed areas included Hermit's Cove (47° 15′ N, 88° 07′ W) and Rabbit Bay (47° 04′ N, 88° 20′ W) in Keweenaw and Houghton counties, respectively. These areas are similarly developed and are comprised predominately of seasonal cottages which are bounded on one side by Lake Superior and on the other by closed-canopy mixed hardwood and boreal transition forest with a gravel road along the forest side of the properties. Cottages at both sites are only on the lake side of the road and have a mixture of old (built prior to 1950) and newer homes, as well as seasonal and permanent residents. Most cottages are occupied primarily during the summer months (Manarolla 2005).

Low-elevation and near-shore portions of the Keweenaw Peninsula are dominated by boreal transition forests composed primarily of paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), red maple (*Acer rubrum*), white spruce (*Picea glauca*), northern white cedar (*Thuja occidentalis*), and yellow birch (*Betula alleghaniensis*). Average precipitation for Keweenaw County during the breeding season from 1 May 2005 through 31 July 2005 was ~22.8 cm with a mean temperature of 14° C (Weather Underground Corporation 2005). The soils of the eastern shore of the Keweenaw Peninsula range from gravelly and rocky sands to sandy loams and are poorly drained in lower elevations near the shore (Albert et al. 1986).

Undeveloped study areas, Smith Fisheries (47° 23′ N, 87° 53′ W), south Rabbit Bay (47° 02′ N, 88° 21′ W), and north Hermit's Cove (47° 15′ N, 88° 06′ W) were selected by visiting areas along the eastern shore in early spring and by using Geographic Information System (GIS) data and aerial photographs to identify areas with and without concentrated residential development near the shore. Undeveloped study areas were along sections of shoreline north of Hermit's Cove and along sections of shoreline south of Rabbit Bay, and were placed ≥300 m from the nearest residential structure. The Smith Fisheries study area was ~48 km north of Hermit's Cove, just north of the town of Lac La Belle, and was only accessible via logging roads and trails (Fig. 1). Thirty-six plots were established for vegetation and bird community sampling, 15 in undeveloped study areas and 21 in developed study areas. We collected data at two spatial scales: (1) broad-scale: developed and undeveloped shoreline study areas, and (2) fine-scale: developed and undeveloped sides of the road accessing developed shoreline study areas.

Measurement of Habitat Variables.—We measured habitat characteristics for the broad scale comparison along transects spaced every 100 m in both developed and undeveloped shoreline study areas. Vegetation transect centers along undeveloped shoreline study areas were 50 m inland. Transects along developed shoreline study areas were centered on the center of the unpaved road (50–75 m from the shore). We considered roads to be part of the vegetation disturbance associated with development. A second set of transects was oriented perpendicular to the shore, and extended 50 m in each direction toward and away from the shoreline for both developed and undeveloped shoreline study areas. This method sampled vegetation in both developed residential property and the undeveloped forest across the road from the development along the developed shoreline. Point-count centers for bird surveys were also placed in the center of the road so that equal

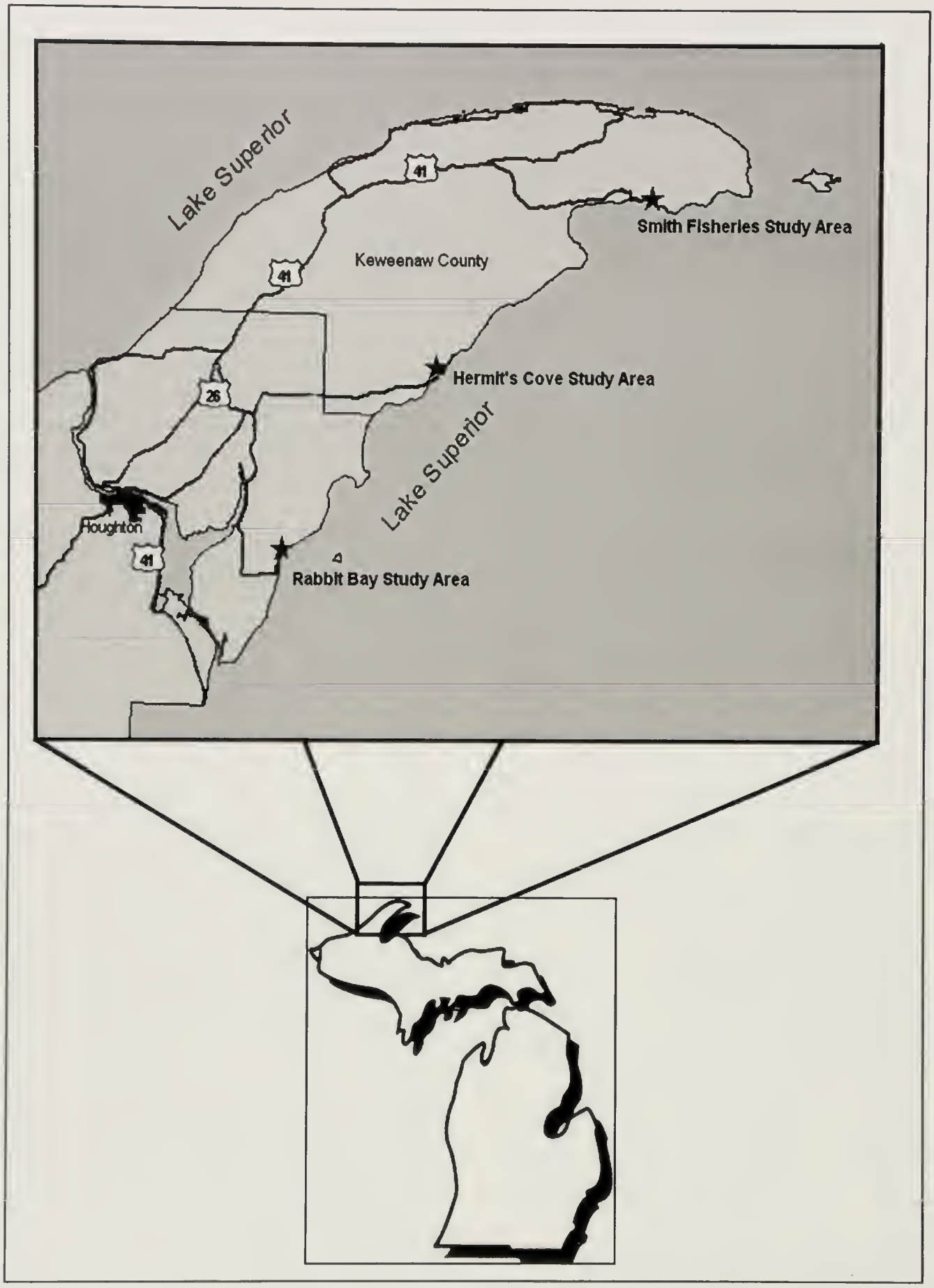

FIG. 1. Study sites in Houghton and Keweenaw counties, Michigan, USA.

portions of the point-count area were in developed/shoreline and undeveloped/inland sides of the road.

Vegetation sampling methods were adapted from Noon (1981). Canopy cover and ground cover were estimated using an ocular tube approximately every 2 m along each transect. Coarse woody debris (CWD) was defined as any piece of downed wood >8 cm in diameter that crossed a transect. The total pieces of CWD that crossed a transect were recorded and divided by the length of the transect (100 m). Diameter at breast height (DBH) and species were recorded for all living trees >3 cm in diameter within arms length, ~0.8 m, on either side of the transect. DBH data were converted to total stem count to compare the number of stems >3 cm in each transect. We also calculated deciduous and coniferous shrub/sapling density along each transect in developed and undeveloped areas. Each woody stem ≤3 cm in diameter at breast height was recorded as either coniferous or deciduous. Average density for each shrub type was calculated as the total number of shrubs counted divided by the length of the transect. Total shrub density was calculated as the sum of both deciduous and coniferous shrubs divided by transect length.

A gridded density board was used to measure understory density and calculate percent cover from 0 to 3 m above the forest floor (Noon 1981). Separate density readings were taken facing areas on each side of the road (i.e., facing the residential development along the shoreline and facing the undeveloped inland) by standing on the side of the road with the density board placed 11.3 m from the road edge. Readings were summed and converted to percent cover in four height categories, 0–0.3, >0.3–1, >1–2, and >2 m, and total understory density 0–3 m.

Bird Surveys.—We used 5 min 50-m fixed-radius point counts to estimate breeding bird relative abundance (Bibby et al. 2000, Sutherland et al. 2004) at developed and undeveloped sites. Counts started at sunrise, ~0600 hrs, and ended by 1030 hrs between 6 June and 1 July 2005. Point-count centers were established every 200 m to minimize double counting individuals (Bibby et al. 2000). Point-count centers in developed shoreline study areas were in the center of the road at the center of vegetation transects, 50–75 m from the shoreline. Point-count centers within undeveloped shoreline study areas were 50 m from the shore to minimize wave noise interference. Twenty-one point-count stations were established in developed shoreline study areas and 15 in undeveloped shoreline study areas; all counts were done by M. T. Ford.

The observer waited for 2 min prior to start of each point-count period (Reynolds et al. 1980). All birds detected by sight or sound within the 50-m radius within 5 min were recorded. Birds detected outside the 50-m radius or seen flying over were also noted, but were not included in analyses. All stations were visited two times in 2005, once early and once later in the breeding season with one of the counts conducted within 30 min of sunrise and the other later in the morning. Point counts were not conducted in rain or high winds (> 20 km/hr) (Robbins 1981).

Bird species richness in developed and undeveloped areas was estimated from the total number of species detected in 2005. Relative abundance for each species was defined as the maximum number of individuals detected between the two visits at each station. Birds were also grouped into nesting/foraging guilds to investigate guild-level associations with development.

Statistical Analysis.—We used *t*- and Wilcoxon-Mann-Whitney non-parametric tests to examine differences in bird abundance and vegetation attributes between developed and undeveloped areas. The more powerful *t*-test was used when substantial deviation from symmetry was not detected in boxplots generated from the raw data (Quinn and Keough 2002). The Wilcoxon-Mann-Whitney test was used at the same significance levels to examine nesting/foraging guild differences between developed and undeveloped areas. Understory density from 0 to 0.3 m and 1 to 2 m appeared to be asymmetrical and was analyzed using Wilcoxon-Mann-Whitney tests. The Shannon-Wiener species diversity index (H') was used to compare species richness and evenness between developed and undeveloped areas (Magurran 2004). All data were tested at a significance level of $\alpha = 0.05$ unless otherwise specified.

RESULTS

Broad Spacial Scale Comparison of Habitat Characteristics in Developed and Undeveloped Shoreline Study Areas.—Developed shoreline had higher deciduous and total shrub density than undeveloped areas. Canopy cover and CWD were

TABLE 1. Vegetation characteristics in developed and undeveloped shoreline study areas on the Keweenaw Peninsula, Michigan.

Characteristics	Treatment	Mean ± SD	*P*
Canopy cover[a]	Developed	76.91 ± 22.33	<0.000
	Undeveloped	87.82 ± 12.08	
Ground cover	Developed	64.68 ± 16.42	0.312
	Undeveloped	61.56 ± 19.16	
Coarse woody debris[a]	Developed	8.38 ± 5.75	<0.000
	Undeveloped	16.6 ± 10.16	
Number of stems > 8 cm[a]	Developed	357 ± 205.96	<0.000
	Undeveloped	288 ± 166.13	
Total shrub density[a]	Developed	6.3 ± 10.62	0.016
	Undeveloped	4.38 ± 9.24	
Deciduous shrub density[a]	Developed	9.38 ± 8.25	<0.000
	Undeveloped	4.35 ± 6.18	
Coniferous shrub density	Developed	3.23 ± 4.16	0.194
	Undeveloped	4.42 ± 6.05	
Total understory density (UD)	Developed	50.03 ± 28.25	0.87
	Undeveloped	50.9 ± 33.21	
UD 0–0.3 m	Developed	78.19 ± 36.31	0.483
	Undeveloped	74 ± 34.17	
UD > 0.3–1.0 m	Developed	51.85 ± 37.2	0.473
	Undeveloped	47.04 ± 40.85	
UD > 1.0–2.0 m	Developed	27.83 ± 34.07	0.203
	Undeveloped	35.63 ± 37.13	
UD > 2.0–3.0 m	Developed	42.24 ± 36.7	0.462
	Undeveloped	46.93 ± 37.88	
Total diameter at breast height (DBH)	Developed	17.77 ± 15.87	0.498
	Undeveloped	19.51 ± 59.66	
DBH of deciduous trees	Developed	16.65 ± 15.18	0.474
	Undeveloped	21.41 ± 96.54	
DBH of coniferous trees	Developed	18.92 ± 16.47	0.635
	Undeveloped	39.4 ± 13.52	

[a] Significant ($\alpha = 0.05$).

greater in undeveloped than developed areas. Developed and undeveloped shoreline study areas did not differ in mean DBH for all trees together, deciduous trees, or coniferous trees. Stem counts were greater in developed than undeveloped shoreline study areas (Table 1).

Small Spatial Scale Comparison of Developed Shoreline and Undeveloped Inland Sides of Shoreline Road.—The residentially developed shoreline side of the road had lower canopy cover, ground cover, CWD, stem counts, total understory density, and understory density from 0–0.3 to >0.3–1 m (Table 2). Mean DBH of coniferous trees, deciduous trees, and all trees pooled did not differ between developed and undeveloped sides of the road (Table 2).

Birds.—We detected 291 individuals of 32 species for all point counts pooled within the 50-m radius point counts during the survey period (Table 3). Species richness was ~34% greater in developed (29 species) shoreline study areas than undeveloped (18 species) shoreline study areas. Ninety percent (29 of 32 species) of all species detected were in developed shoreline study areas; only 56% (18 of 32 species) of all species detected were in undeveloped shoreline study areas. Fourteen species were found only in developed shoreline study areas and three species were only in undeveloped shoreline study areas (Table 3). The Shannon-Wiener diversity index (H') was 2.96 in developed and 2.45 in undeveloped shoreline study areas. Species evenness was virtually identical in developed ($E = 0.88$) and undeveloped ($E = 0.86$) shoreline study areas.

The Shannon-Wiener diversity index within developed shoreline study areas was 2.97 on the developed side of the road and 2.70 on the inland, undeveloped side of the road. Species evenness was similar between shoreline ($E = 0.92$) and inland ($E = 0.87$) sides of the road.

TABLE 2. Vegetation characteristics in developed shoreline and undeveloped inland sides of shoreline access roads in residentially developed areas on the Keweenaw Peninsula, Michigan.

Characteristics	Treatment	Mean ± SD	*P*
Canopy cover[a]	Shoreline	69.49 ± 23.31	0.002
	Inland	84.34 ± 18.79	
Ground cover[a]	Shoreline	68.16 ± 18.9	0.005
	Inland	69.49 ± 12.81	
Coarse woody debris[a]	Shoreline	6.71 ± 6.16	0.008
	Inland	10.05 ± 4.83	
Number of stems > 8 cm[a]	Shoreline	138 ± 79.53	<0.001
	Inland	219.5 ± 126.5	
Total shrub density	Shoreline	5.51 ± 6.99	0.16
	Inland	7.1 ± 6.66	
Deciduous shrub density	Shoreline	7.71 ± 8.07	0.066
	Inland	11.05 ± 8.19	
Coniferous shrub density	Shoreline	3.32 ± 4.79	0.854
	Inland	3.15 ± 3.48	
Total understory density[a]	Shoreline	43.86 ± 39.86	0.047
	Inland	56.2 ± 40.33	
UD 0–0.3 m[a]	Shoreline	67.88 ± 40.81	0.01
	Inland	88.5 ± 28.06	
UD > 0.3–1.0 m[a]	Shoreline	41.11 ± 35.9	0.008
	Inland	62.59 ± 35.73	
UD > 1.0–2.0 m	Shoreline	25.32 ± 32.19	0.508
	Inland	30.34 ± 36.08	
UD > 2.0–3.0 m	Shoreline	41.12 ± 35.07	0.784
	Inland	43.37 ± 38.67	
Total diameter at breast height (DBH)	Shoreline	18.75 ± 16.21	0.194
	Inland	17.15 ± 15.64	
DBH of deciduous trees	Shoreline	18.13 ± 14.13	0.21
	Inland	15.97 ± 15.63	
DBH of coniferous trees	Shoreline	19.2 ± 17.56	0.77
	Inland	18.68 ± 15.55	

[a] Significant ($\alpha = 0.05$).

Broad Spatial Scale Comparison of Bird Species Relative Abundance.—Only Red-eyed Vireos (*Vireo olivaceus*), of 32 total species detected, were significantly (5 times) more abundant in developed than undeveloped shoreline study areas. Ground-nesting birds were equally abundant in developed and undeveloped shoreline study areas ($P > 0.05$). Shrub nesters were more abundant in undeveloped forest and canopy nesters were more abundant in developed shoreline study areas when species were pooled based on nest site location ($P < 0.05$) (Table 3).

Fine-scale Comparison of Bird Species Relative Abundance.—Two species, American Crow (*Corvus brachyrhynchos*) and American Robin (*Turdus migratorius*) were statistically more abundant on the developed, shoreline side of the shoreline access roads. Three species, Black-throated Green Warbler (*Dendroica virens*), Red-eyed Vireo, and Red-breasted Nuthatch (*Sitta canadensis*) were more abundant on the undeveloped, inland side of shoreline access roads (Table 4). Differences in relative abundance of American Redstarts (*Setophaga ruticilla*) and Blackburnian Warblers (*Dendroica fusca*) approached significance ($P = 0.10$) with both detected more frequently on the undeveloped, inland side of point counts (Table 4).

DISCUSSION

Analyses of developed and undeveloped shoreline areas at the broad scale showed that only one species was significantly more abundant in developed shoreline areas and no species were significantly more abundant in undeveloped shoreline areas. Fine-scale plot-level analyses in developed areas suggested that two species were significantly more abundant on the developed,

TABLE 3. Bird species detected on point counts between May and July 2005 in developed and undeveloped study areas on the Keweenaw Peninsula, Michigan.

Common name	Species	AOU Code	Number of individuals detected		Nesting guild		
			Developed	Undeveloped	Ground	Shrub	Canopy
American Crow	*Corvus brachyrhynchos*	AMCR	5	0			x
American Goldfinch	*Spinus tristis*	AMGO	1	0		x	
American Redstart	*Setophaga ruticilla*	AMRE	14	10			x
American Robin	*Turdus migratorius*	AMRO	9	0			x
Black-and-white Warbler	*Mniotilta varia*	BAWW	7	3	x		
Black-capped Chickadee	*Poecile atricapillus*	BCCH	6	0			x
Blackburnian Warbler	*Dendroica fusca*	BLBW	1	0			x
Blue Jay	*Cyanocitta cristata*	BLJA	2	1			x
Black-throated Green Warbler	*Dendroica virens*	BTNW	7	3			x
Chipping Sparrow	*Spizella passerina*	CHSP	3	0		x	
Cape May Warbler	*Dendroica tigrina*	CMWA	0	1			x
Common Raven	*Corvus corax*	CORA	0	2			x
Chestnut-sided Warbler	*Dendroica pensylvanica*	CSWA	1	0		x	
Golden-crowned Kinglet	*Regulus satrapa*	GCKI	6	1			x
Hairy Woodpecker	*Picoides villosus*	HAWO	2	0			x
Hermit Thrush	*Catharus guttatus*	HETH	3	10	x		
Mallard	*Anas platyrhynchos*	MALL	2	0	x		
Magnolia Warbler	*Dendroica magnolia*	MAWA	1	1			x
Yellow-rumped Warbler	*D. coronata*	MYWA	18	4			x
Nashville Warbler	*Vermivora ruficapilla*	NAWA	23	24	x		
Northern Parula	*Parula americana*	NOPA	24	12			x
Ovenbird	*Seiurus aurocapilla*	OVEN	9	0	x		
Pine Warbler	*Dendroica pinus*	PIWA	3	0			x
Red-breasted Nuthatch	*Sitta canadensis*	RBNU	5	3			x
Ruby-crowned Kinglet	*Regulus calendula*	RCKI	0	1			x
Red-eyed Vireo	*Vireo olivaceus*	REVI	14	3			x
Ruby-throated Hummingbird	*Archilochus colubris*	RTHU	2	0			x
Song Sparrow	*Melospiza melodia*	SOSP	1	0	x		
Swainson's Thrush	*Catharus ustulatus*	SWTH	3	8			x
White-throated Sparrow	*Zonotrichia albicollis*	WTSP	7	0	x		
White-breasted Nuthatch	*Sitta carolinensis*	WBNU	1	0			x
Winter Wren	*Troglodytes troglodytes*	WIWR	6	13		x	

shoreline portion rather than the undeveloped, inland portion of the shoreline access roads. Three species were more abundant on the inland, undeveloped side of the shoreline access roads. Our results suggest species may be responding to habitat alterations associated with residential development at the patch, rather than the larger stand/landscape scale. We found development-related differences in natural habitat features including canopy volume, shrub cover, forest floor vegetative cover, and amount of CWD.

Riparian areas in much of the U.S. represent concentrations of biodiversity and foci for residential development in rural areas (Naiman et al. 1993, Schnaiberg et al. 2002, Bub et al. 2004, Gonzalez-Abraham et al. 2006). Shoreline vegetation, compared to adjoining inland sites, is typically denser, more varied in species composition, and offers greater vertical and horizontal structural diversity (Riffell et al. 2001). Rottenborn (1999) proposed that shoreline forests have unique vegetation characteristics compared to similar forests distant from the shoreline and these differences may shape patterns of bird community composition. Research has shown that riparian vegetation structure influences breeding bird communities (Willson 1974, Hostetler and Holling 2000) and altering these habitats through removal of native vegetation can change bird community structure. Vegetation structure fre-

TABLE 4. Birds detected on undeveloped inland and developed shoreline sides of shoreline access roads in residentially developed areas on the Keweenaw Peninsula, Michigan.

Species	Treatment	Total count	Mean/10 plots ± SD	Zcalc[a]
AMCR[a]	Inland	0	0 ± 0	2.03
	Shoreline	5	23.8 ± 0.54	
AMGO	Inland	0	0 ± 0	0.97
	Shoreline	1	4.8 ± 0.22	
AMRE	Inland	17	33.3 ± 0.66	1.91
	Shoreline	7	28.6 ± 0.56	
AMRO	Inland	1	0 ± 0	1.97
	Shoreline	8	38.1 ± 0.74	
BCCH	Inland	1	4.8 ± 0.22	1.37
	Shoreline	4	19 ± 0.4	
BLBW	Inland	2	9.5 ± 0.3	1.74
	Shoreline	0	0 ± 0	
BLJA	Inland	1	4.8 ± 0.22	1.01
	Shoreline	2	9.5 ± 0.3	
BTNW[a]	Inland	6	28.6 ± 0.56	2.04
	Shoreline	2	9.5 ± 0.3	
BAWW	Inland	3	14.3 ± 0.36	0.04
	Shoreline	5	23.8 ± 0.44	
CHSP	Inland	1	4.8 ± 0.22	0.57
	Shoreline	2	9.5 ± 0.3	
CSWA	Inland	0	0 ± 0	0.97
	Shoreline	1	4.8 ± 0.22	
CORA	Inland	0	0 ± 0	1.4
	Shoreline	0	5.6 ± 0.23	
GCKI	Inland	4	19 ± 0.4	1.17
	Shoreline	2	9.5 ± 0.3	
HAWO	Inland	1	4.8 ± 0.22	−0.02
	Shoreline	1	4.8 ± 0.22	
HETH	Inland	0	0 ± 0	0.2
	Shoreline	2	9.5 ± 0.3	
MALL	Inland	0	0 ± 0	0.97
	Shoreline	2	9.5 ± 0.44	
MAWA	Inland	1	4.8 ± 0.22	1.4
	Shoreline	0	0 ± 0	
NAWA[a]	Inland	14	70 ± 0.66	4.2
	Shoreline	8	38.1 ± 0.59	
NOPA[a]	Inland	21	100 ± 0.95	4.02
	Shoreline	4	19 ± 0.4	
OVEN	Inland	6	28.6 ± 0.64	0.45
	Shoreline	3	14.3 ± 0.36	
PIWA	Inland	1	4.8 ± 0.22	−0.02
	Shoreline	1	4.8 ± 0.22	
RBNU[a]	Inland	4	19 ± 0.4	2.22
	Shoreline	1	4.8 ± 0.22	
REVI[a]	Inland	10	47.6 ± 0.51	2.47
	Shoreline	4	19 ± 0.40	
RCKI	Inland	1	2.8 ± 0.17	0.97
	Shoreline	0	0 ± 0	
RTHU	Inland	2	9.5 ± 0.30	1.40
	Shoreline	0	0 ± 0	
SOSP	Inland	0	0 ± 0	1.4
	Shoreline	2	9.5 ± 0.3	
SWTH	Inland	2	9.5 ± 0.3	0.7
	Shoreline	1	4.8 ± 0.22	
WBNU	Inland	1	4.8 ± 0.22	0.97
	Shoreline	0	0 ± 0	
WIWR[a]	Inland	5	24 ± 0.44	3.58
	Shoreline	1	5 ± 0.22	
WTSP	Inland	3	14 ± 0.36	0.73
	Shoreline	5	24 ± 0.44	
MYWA	Inland	10	48 ± 0.68	0.71
	Shoreline	9	43 ± 0.51	

[a] Mann Whitney Zcrit = 1.96 at $\alpha = 0.05$ and Zcrit = 1.645 at $\alpha = 0.10$. Ho is rejected when Zcalc > Zcrit.

quently influences bird species richness, relative abundance (Willson 1974, Hostetler and Holling 2000), and foraging behavior (Smith et al. 1998). We found development-related differences in natural habitat features including canopy volume, shrub cover, forest floor vegetative cover, and amount of CWD. Research has shown that natural habitat features such as canopy volume, shrub cover, and forest vegetative cover are influenced by residential development (Clark et al. 1984, Christensen et al. 1996, Woodford and Meyer 2003). Many studies (Willson 1974, Burke and Nol 1998, Sallabanks et al. 2000) have suggested that changes in the avian community in the presence of human development are the result of development-related changes in vegetation rather than direct human disturbance of birds.

Elias and Meyer (2003) found that undeveloped shoreline in northern Wisconsin had higher percent canopy, subcanopy, understory cover, coarse woody debris, and percentage of shoreline overhung by trees and shrubs compared to developed shoreline stretches. They also found that plant species richness and diversity were greater in developed than in undeveloped shoreline areas. Lindsay et al. (2002) compared bird community attributes in riparian areas along developed and undeveloped inland lakes in northern Wisconsin. They reported that granivorous and omnivorous bird species were more abundant along developed lakes than undeveloped lakes. In contrast, insectivorous species were more abundant along undeveloped than developed lakeshores (Lindsay et al. 2002). Rottenborn (1999) reported that shoreline development near riparian areas in California affected nearby riparian bird communities and concluded that

species richness and diversity decreased as native vegetation was lost to residential development.

Differences in vegetation characteristics between developed and undeveloped shoreline areas may be responsible for most of the differences we observed in bird abundance. Deciduous shrub density and total shrub density were greater along developed shoreline, while mean canopy cover and mean number of CWD pieces were greater along undeveloped shoreline. The greater number of all but coniferous shrubs and saplings within developed shoreline areas is likely the result of greater light penetration from the more open forest canopy. Comparison of forest characteristics at the individual plot scale suggested that within-plot canopy cover, CWD, understory density from 0 to 0.3 m, >0.3 to 1 m, and overall understory density were greater on the undeveloped side of shoreline access roads. The presence of development features such as lawns, houses, outbuildings, walkways and driveways may contribute to these differences.

Christiansen et al. (1996) found that inland lake shoreline areas in northern Wisconsin with more cabins had fewer large pieces of dead and down wood in near shore waters, and speculated that many property owners remove snags and downed wood in or near the water's edge. The same process may occur around cottages, decreasing the amount of CWD in these areas. All study areas have thin soils which, given the close proximity to winds off Lake Superior, may result in increased blow-downs in developed shoreline areas, heightening the contrast in CWD abundance between developed and undeveloped shorelines.

The higher abundance of CWD, canopy cover, understory density from 0 to 0.3 m and from >0.3 to 1.0 m available in the undeveloped inland side of shoreline access road census locations likely influenced the relative abundance of several species. Nashville Warblers (*Vermivora ruficapilla*) and Winter Wrens (*Troglodytes troglodytes*) were both more abundant in the undeveloped inland portion of shoreline access roads. Nashville Warblers nest at the ground level and Winter Wrens often place their nests in the roots of upturned trees or snags (Ehrlich et. al. 1988). The higher abundance of CWD and increased understory density on the undeveloped, inland side of the road may be important habitat features for these two species.

Northern Parula (*Parula americana*) have been shown to prefer riparian areas (Moldenhauer and Regelski 1996) and to be relatively tolerant of habitat disturbance short of clear cutting (Brooks 1940). Northern Parula, which build nests in the mid-canopy, have been shown to be positively correlated with at least 75% canopy cover and, when breeding, are heavily dependent on an abundance of epiphytes, particularly lichen (*Usnea* spp.) in their northern range (Collins et al. 1982, Moldenhauer and Regelski 1996). Northern Parula were more abundant on the inland, undeveloped side of shoreline access roads than on the residentially developed side. This may be the result of lower abundance of epiphytic lichen related to canopy openings (Esseen and Rehhorn 1998) and/or preference by Northern Parula for increased canopy cover, which was greater on the inland side of point-count plots.

Red-breasted Nuthatches depend on the availability of cavities in dead standing trees or roots of upturned trees as well as sap from living conifers. The sap is used to coat the entrance of the cavity during the incubation period to protect against nest predators (Ghalambor and Martin 1999). The increased abundance of CWD in inland areas may be an indicator of dead, dying trees in the vicinity and perhaps of standing dead, cavity bearing trees making it an increasingly suitable habitat for Red-breasted Nuthatches.

Given that our data were collected over a single year, we realize there are several limitations associated with our conclusions. Annual variations in weather, vegetation characteristics associated with development (i.e., possible collection of CWD by landowners for firewood or annual maintenance of vegetation within residential properties), and local bird community all likely contribute to bird species response within our study areas. Another recognized limitation is the potential for birds to naturally nest >50 m from the shoreline, regardless of the presence of residential development. Species detection is another factor which may be identified as a limitation of our study; it is likely that differences exist in detection of bird species between the more open, less vegetated residential shoreline areas and undeveloped areas with overall greater sub-canopy density. We believe the differences found in bird species abundance between residentially developed and undeveloped shoreline areas are legitimate based upon the known species habitat preferences and the measured vegetation characteristics of each study area.

It is essential to clarify the scale at which bird species respond to changes related to shoreline development to understand how development-related habitat alteration interacts with breeding bird habitat use. Our results suggest birds may respond more to development-related habitat changes at the scale of tens of meters, than at the scale of the shoreline study areas we measured (i.e., hundreds of meters).

Ornithologists and ecologists have long recognized the role that scale has in understanding habitat use in wildlife (Wiens 1989, Levin 1992). The differing patterns of species composition and relative abundance we found suggest development related changes did not elicit a strong response by most bird species at the scale of the 1 km shoreline. However, development related changes likely influence which areas (e.g., developed or undeveloped side of the road) within a shoreline area a bird chooses for breeding. Our study was conducted in a landscape matrix that is >95% forested, and any forest opening related to residential development represents a relatively small landscape disturbance. Landscape condition has also been shown to be a strong predictor of bird species presence (Saab 1999, Lee et al. 2002). Our results should be viewed in the context of the largely unfragmented surrounding forest.

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SONGBIRD NEST SURVIVAL IS INVARIANT TO EARLY-SUCCESSIONAL RESTORATION TREATMENTS IN A LARGE RIVER FLOODPLAIN

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ABSTRACT.—We monitored songbird nest survival in two reforesting, ~50-ha former cropland sites along the Missouri River in central Missouri from 2001 to 2003. Sites were partitioned into three experimental units, each receiving one of three tree planting treatments. Nest densities varied among restoration treatments for four of five species, but overall nest survival rates did not. Nest survival varied with day-of-year and with incidence of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Nest survival was higher early and late in the season, and parasitized nests experienced lower nest survival, despite few complete losses directly attributable to parasitism. Probability of parasitism was inversely related to distance to the nearest tree, and was much lower than in old field study sites in the same region. High cowbird parasitism frequencies are usually associated with landscapes low in forest cover, yet these sites in an agriculturally-dominated bottomland landscape experienced low (~0.8–24%) cowbird parasitism. The assumed negative relationship between landscape-level forest cover and cowbird parasitism needs further study in habitats other than forest. *Received 1 September 2008. Accepted 26 November 2009.*

Studies of nest predation have noted variation in nesting success among habitat types within the same species or suites of species (McCoy et al. 1999, Lloyd and Martin 2005), or variation in nesting success among regions or fragment sizes (Donovan et al. 1995, Robinson et al. 1995). These differences could be attributed to predators, which are known to vary across regions (Thompson et al. 1999, Pietz and Granfors 2000). Predator identities may vary across habitat types within the same landscape or region (Chalfoun et al. 2002), although predator differences may not be reflected in differences in nesting success (Thompson and Burhans 2003).

Nest predation is considered the largest cause of nest loss (Ricklefs 1969, Martin 1992), and Brown-headed Cowbird (*Molothrus ater*) brood parasitism, which also affects nest success, may also vary by region, landscape, or habitat type (Robinson et al. 1995, Burhans 1997, Burhans and Thompson 2006). Much of our present understanding about the interactions of habitat and landscape features affecting cowbird parasitism comes from studies in upland forested habitats (Brittingham and Temple 1983, Robinson et al. 1995, Donovan et al. 2000, Thompson et al. 2000).

We monitored songbird nesting success at two sites having three contiguous 16.2-ha habitats of former cropland along the Missouri River. The habitats varied in densities of planted oaks (*Quercus* spp.) and in presence of a homogenous herbaceous cover crop. The treatments were sufficiently large to attract reasonable numbers of species of nesting birds across the different habitat types. Habitats were physically adjacent to one another, so that any differences in predation within the site should have been attributable to variation in habitat type only, and not to factors such as region, landscape context, or fragmentation. Our specific goals were to examine: (1) whether nesting success varied among the planted habitat types, and (2) whether frequencies of cowbird parasitism varied among habitat types.

METHODS

Our central Missouri, USA research sites were managed by the Missouri Department of Conservation and were in predominately agricultural floodplain landscapes surrounded by agriculture or early-successional vegetation originating from floods of the mid-1990s. Plowboy Bend Conservation Area (38° 48′ 05″ N, 92° 24′ 17″ W) was a row-crop agriculture/floodplain ecosystem west of the Missouri River's main channel within a levee-protected floodplain. The surrounding landscape within a 5-km radius (Driscoll and Donovan 2004) centered on Plowboy Bend was ~24% cropland,

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26% grassland, 34% forest, and 15% water (based on circa-2000 TM satellite data interpreted by the Missouri Resources Assessment partnership; www.cerc.usgs.gov/morap). Smoky Waters Conservation Area (38° 35′ 09″ N, 91° 58′ 03″ W) was 72 km southeast of Plowboy Bend between the main channels of the Missouri and Osage rivers (a major tributary of the Missouri River). The surrounding landscape within a 5-km radius was ~24% cropland, 23% grassland, 33% forest, and 18% water. The floodplain at Smoky Waters is subject to occasional flooding and has not been protected since a levee was breached in the 1993 and 1995 floods. Smoky Waters was flooded for 3 weeks in June 2001, and Plowboy Bend was flooded for 1 week during the same time period; Smoky Waters was also flooded for 1 week in early May 2002.

The three 16.2-ha restoration treatment units at each site were cleared of herbaceous vegetation and disked in autumn 1999. Two of the three units were planted with swamp white oak (*Quercus bicolor*) and pin oak (*Q. palustris*) at a 9 × 9-m spacing (Dey et al. 2001, Shaw et al. 2003). Redtop grass (*Agrostis gigantea*) was planted in one of the two units, producing a low, dense ground cover that substantially reduced invasion of other herbaceous and woody vegetation. We refer to the combination of planted oaks and redtop grass as the ''redtop'' treatment. The ''no redtop'' treatment contained the same oak plantings, but without seeded ground cover, and had diverse mixtures of invasive herbaceous and woody growth compared to redtop habitats. The remaining unit at each site served as a ''control'' and was not planted to either oak or redtop (Shaw et al. 2003). Structurally, vegetation in the control treatments was most similar to that in the no redtop treatments except for the absence of oaks. Planted oaks included conventional 1-year old, not transplanted bare root seedlings, but also included ''RPM®'' (Root Production Method) oaks. These oaks were grown with a special root-pruning method and attaincd heights of ≥1.5 m within the first year of planting (Grossman et al. 2003, Dey et al. 2004). Both sites received the same three plantings in the same arrays but, at Plowboy Bend, the three units adjoined each other in a ''pyramid'' fashion, whereas at Smoky Waters they were adjoined linearly (redtop, no redtop, control).

Nest Monitoring.—We searched for and monitored nests from late April to early August during 2001–2003. Nests were located by systematically searching potential nest sites and by observing behavior of adult birds (Martin and Geupel 1993). We devoted equal time to searching in each treatment unit, alternating searches among the three habitats according to visit and time of day within each site.

We marked nest locations with plastic flagging placed ≥3 m from the nest. We focused on Dickcissel (*Spiza americana*), Field Sparrow (*Spizella pusilla*), Indigo Bunting (*Passerina cyanea*), Red-Winged Blackbird (*Agelaius phoeniceus*), and Song Sparrow (*Melospiza melodia*) because they were the most common nesters at the sites. We monitored nests on average every 3–4 days except during flooding in 2001 and 2002. We found nests of the five focal species in building (22%), laying (20%), incubation (46%), and nestling (12%) stages.

We visited nests in early morning on the expected fledging date (based upon observed date of hatching or estimated age of nestlings) to look for evidence of fledging, such as fledgling begging calls, observation of fledglings, parents carrying food to fledglings, or parents chipping rapidly nearby. Nests found empty prior to this date were considered depredated unless we observed evidence of premature fledging. Nests were considered ''successful'' if they fledged at least one chick; fates of nests where we did not observe these activities were classified as ''unknown'' for the last interval between visits; this interval was censored to not bias the analysis (Stanley 2004). We approached nests and viewed their contents at the maximum distance possible (~2 to 4 m) to ascertain status, and were careful not to leave ''dead end trails'' leading to the nest (Martin and Geupel 1993). Interval fates other than ''successful'' and ''depredated'' included ''abandoned'' and ''flooding.'' Nest failures due to cowbird brood parasitism were from parental desertion (eggs remaining in abandoned parasitized nest) or complete brood loss after parasitism (starvation of host chicks or complete absence of host chicks or eggs in parasitized nests) and were classified as ''cowbird.'' ''Disturbance'' included cases where nests were tipped or removed from the substrate, presumably due to wind or animal trampling, but the nest contents remained on the ground.

Vegetation Measurements.—We used vertical density-board measurements taken between 20 June and 8 July in 2002 from 72 systematically

placed locations in each treatment. Vegetation data were collected in other years, but we chose 2002 data because samples were most complete in that year, and because 2002 represented a temporal midpoint in the study. Percent cover of vertical vegetation was estimated using a nine-increment density board (2.25 m tall × 0.25 m wide). Percent cover of living and dead vegetation was estimated at each 0.25-m increment from a distance of 15 m. We estimated percent cover in each increment for forb, grass, and woody vegetation, combining them to generate an estimate of mean total percent cover for each board measurement. Grand means were calculated for each sample over all of the 0.25-m increments for each vegetation type of interest (forb, grass, and total vertical vegetation). We focused on grass cover, forb cover, and grass height because visually these differences appeared to distinguish treatments from each other (despite the presence of planted oaks, woody cover was negligible within all treatments because the young seedlings were small). We added a category for "grass cover <0.25 m" using only the grass scores from the lowest increment to quantify low dense grass cover, which appeared to visually distinguish redtop treatments from other treatments in the field. We also added "Mean grass height," which was the last-recorded increment having grass cover on the vertical density board. We randomly chose 68 of the 72 vegetation samples in each site X treatment combination due to inconsistent numbers of samples taken in each treatment.

We measured the distance from ground to the bottom of the nest cup (±0.01 m; hereafter nest height) upon finding each nest because nests were, at times, toppled after predation. Nest height was measured in 0.01-m increments with marked sticks that were carried daily for nest-searching. We obtained the spatial coordinates (Universal Transverse Mercator) after termination of nesting using a Trimble Geoexplorer Global Positioning System (GPS) unit with an accuracy of 5–7 m. We measured the distance between each nest and the nearest tree (≥3 m in estimated height) using a Geographic Information System (GIS) to compare nest locations with locations of previously mapped trees and forest patches.

Data Analysis.—We used a general linear model (Proc MIXED, SAS Version 9.1, 2003) with an LSMEANS statement to calculate means and standard errors for each vegetation variable of interest. We included site as a random effect to account for differences between the two sites. We used Likelihood Ratio Tests to assess overall model significance against a null model that included only the intercept; we performed multiple comparisons tests for differences in least squares means among the three treatment types using a Bonferroni adjustment if the overall model was significant ($P \leq 0.05$).

We investigated whether nest densities varied among restoration treatments by comparing observed numbers of nests in each habitat to expected numbers under the assumption of no difference among restoration treatments. We used Chi-square goodness-of-fit tests to assess statistical significance ($P < 0.05$).

We used the logistic-exposure method (Shaffer 2004) to estimate and analyze nest survival. This approach uses a generalized linear model with binomial distribution (interval nest fate = 0 if failed and 1 if successful) and logit link function to model daily nest survival in terms of covariates potentially affecting nest survival (Dinsmore et al. 2002, Shaffer 2004). We treated each interval between nest checks as an observation, thereby allowing time-dependent covariates such as nest stage to change from one interval to the next during the nesting cycle (Shaffer 2004). We did not include observation days of building stage nests in the analysis. Intervals between nest observations were usually >1 day and varied in length, and we used the modified logit link function: $g(\theta) = \log_e (\theta^{1/t}/[1 - \theta^{1/t}])$, where θ is the interval survival rate and t is the interval length in days (Shaffer 2004). The effective sample size, which follows from the model likelihood, is the sum of the total number of days that all nests were known to have survived and the number of intervals that ended in failure (Rotella et al. 2004). We used the GENMOD procedure in SAS (SAS Institute 2000) to estimate parameters of the logistic-exposure models.

We developed *a priori* candidate models involving (1) covariates related to our hypothesis about effects of the restoration treatment on nest survival, and (2) additional covariates that we believed might explain variation in nest survival (below).

- Restoration treatment, which was defined as control, redtop, or no redtop.
- Nest height, which has been positively related to nest survival for some of the same species in other studies in the region (Burhans et al. 2002, Burhans and Thompson 2006).

— Nesting stage, for which we considered the stage (laying, incubation, nestling) confirmed at the terminal visit of the interval to be the stage for that interval; e.g., if a nest transitioned from incubation to the nestling stage during an interval, a value of "nestling" was assigned to that interval.

— Day-of-year, which may reflect seasonal variation in predator activity or abundance. We included both linear and quadratic terms (day-of-year, [day-of-year]^2), the latter term to account for non-linear nest survival over the season in models with "day-of-year" (Grant et al. 2005).

— Cowbird parasitism, which presumably affects nest predation because of increased begging calls and nest visits by hosts and/or cowbirds, which alerts predators to the presence of nests (Dearborn et al. 1998, Hauber 2000).

— Year, site (Plowboy Bend or Smoky Waters), bird species, and site were included as categorical covariates to account for additional unexplained variation.

We considered models that corresponded to the covariates and reflected our hypotheses about relationships of habitat and other factors to nest survival: (1) day-of-year, (2) cowbird parasitism, (3) nest height, (4) nesting stage, and (5) habitat. Each model also included species, year, site, and year × site to reflect our study design and to reduce the chance of statistical confounding. We also considered a model that included only species, year, site, and year × site, and a global model that included all covariates.

Nests were considered "successful" for the relevant interval if at least one young fledged. We considered complete nest losses due to nest predation, flooding, unknown weather events, or apparent trampling by animals, abandonment, or cowbird parasitism to be "failed" nesting attempts. Only one nest fledged a cowbird but not host young; it was considered "successful" for the interval for which it fledged the cowbird.

We evaluated support by comparing multiple models, fit to the same data, using an information-theoretic approach (Burnham and Anderson 2002). We considered the model with the lowest value for Akaike's Information Criterion (AIC) to be the best approximating model for the data, and considered models within two AIC units of the best model to represent potential best models (Burnham and Anderson 2002). However, we report 95% confidence intervals (CIs) for each parameter estimate based on model-averaging to account for model-selection uncertainty (Burnham and Anderson 2002). We used model-based methods (Shaffer and Thompson 2007) to estimate nest survival (including 95% CIs) in relation to covariates.

We computed species-specific period survival to show model-based relationships over the entire nest period in terms of the covariates by raising daily survival to a power equal to the average length of the nest cycle for each species (Field Sparrow = 23 days; Dickcissel = 25.5 days; Indigo Bunting, Red-winged Blackbird, Song Sparrow = 27 days; Ehrlich et al. 1988; D. E. Burhans, unpubl. data). We realize this average does not correspond to the exact nest cycle for each species, but it is close for most of the species, and our goal was to simplify graphic interpretation of model-based results. We show model-based relationships between 26-day period survival rates and covariates other than species by weighting the daily survival rate estimate for each species by the proportion of observed nests of that species. We computed model-averaged survival estimates for a given covariate by holding remaining covariates at their mean value. We calculated period mortality due to a specific cause (abandonment, predation, parasitism, disturbance) by multiplying the model-based average period mortality rate (1 − average period survival) by the proportion of nests in that category; for example, if the average period mortality over all nests was 0.75 and the proportion of abandoned nests was 0.10, period mortality due to abandonment would be estimated as $0.10 \times 0.75 = 0.075$.

We used logistic regression to model the probability of cowbird parasitism, including only nests initiated by the second week of July, as cowbirds typically do not lay after this time in this region (Burhans 1997). We included bird species in each of the models similar to the nest survival models. Models included: (1) species only, (2) habitat (redtop, no redtop, control) and species, (3) site (Plowboy Bend or Smoky Waters) and species, (4) year and species, and (5) a global model with all of the above covariates. We also considered (6) a model incorporating distance to the nearest tree (≥3 m in estimated height; range = 1–263 m.). Parasitism probability has been negatively associated with distance to the nearest tree in other studies (Clotfelter 1998), presumably because female cowbirds are known to survey for

TABLE 1. Distribution of nests across restoration treatments for five songbird species in lower Missouri River floodplains, 2001–2003. Chi-square tests (df = 2, all tests) were used to assess whether nest number and densities varied with restoration treatment.

Species	Restoration treatment			χ^2	P
	Redtop	No redtop	Control		
Dickcissel	22	37	8	18.84	<0.001
Field Sparrow	23	5	22	12.28	0.002
Indigo Bunting	5	31	25	18.23	<0.001
Red-winged Blackbird	70	143	40	66.55	<0.001
Song Sparrow	9	15	8	2.69	0.26

host nests from trees (Hauber and Russo 2000, Saunders et al. 2003).

RESULTS

We analyzed data from 463 nests representing an effective sample size of 4,773. This represented 67 Dickcissel nests (daily survival estimate assuming constant survival = 0.941; CI = 0.913–0.960), 50 Field Sparrow nests (0.958; 0.930–0.975), 61 Indigo Bunting nests (0.957; 0.934–0.972), 253 Red-winged Blackbird nests (0.951; 0.936–0.962), and 32 Song Sparrow nests (0.933; 0.888–0.961). Estimated daily survival rate of all species combined under the assumption of constant survival was 0.950 (CI = 0.939–0.959) and average period survival over the entire nesting cycle was 0.26. Thus, average period mortality across the entire nest cycle from all sources was 0.74. Predation (215 losses) accounted for 63% of period mortality. Flooding (18 losses; 5%); abandonment, including that attributable to cowbirds (11 losses, 3%); and unknown (weather or animal trampling) events (9 losses, 3%) accounted for additional mortality. Complete nest losses due to cowbird parasitism occurred only through abandonment with desertions at one Field Sparrow nest and three Indigo Bunting nests (1%). Nests were not equally distributed among restoration treatments for all species except Song Sparrow (Table 1).

The best approximating model of nest survival was that with parasitism (Table 2; model-estimated period survival for parasitized nests: 0.10, CI = 0.00–0.40; unparasitized nests: 0.27, 0.19–0.35). Day-of-year and global models also received support (Table 2). We found only weak support for differences in nest survival attributable to restoration treatment (Table 2, Fig. 1B). The site × year and species covariates were not related to specific hypotheses, but we include graphs of the model-averaged values to show the considerable variation (Fig. 1C, D).

Cowbird Parasitism.—We analyzed 426 nests for probability of cowbird parasitism. Cowbird

TABLE 2. Candidate models of daily nest survival for five songbird species in lower Missouri River floodplains, 2001–2003. Models with a lower ΔAIC and a greater Akaike weight (w_i) have greater support; K is the number of parameters in the model.

Model	Variables	K	AIC	ΔAIC	w_i
Parasitism	Year × Site, Year, Site, Species, Parasitism[a]	11	1380.73	0	0.52
Day-of-year	Year × Site, Year, Site, Species, Day-of-year[b]	12	1382.06	1.34	0.27
Global	Year × Site, Year, Site, Species, Parasitism[a], Day-of-year[b], Nest height, Nesting stage, Habitat	18	1383.98	3.33	0.10
Species	Year × Site, Year, Site, Species	10	1385.29	4.55	0.05
Nest height	Year × Site, Year, Site, Species, Nest height	11	1386.74	6.01	0.03
Nesting stage	Year × Site, Year, Site, Species, Nesting stage (laying, incubation, nestling)	12	1387.51	6.79	0.02
Restoration treatment	Year × Site, Year, Site, Species, Restoration treatment (redtop, no redtop, control)	12	1388.28	7.56	0.01
Null		1	1420.55	39.76	0.00

[a] Unparasitized = 0; parasitized = 1.
[b] Includes day-of-year, (day-of-year)^2.

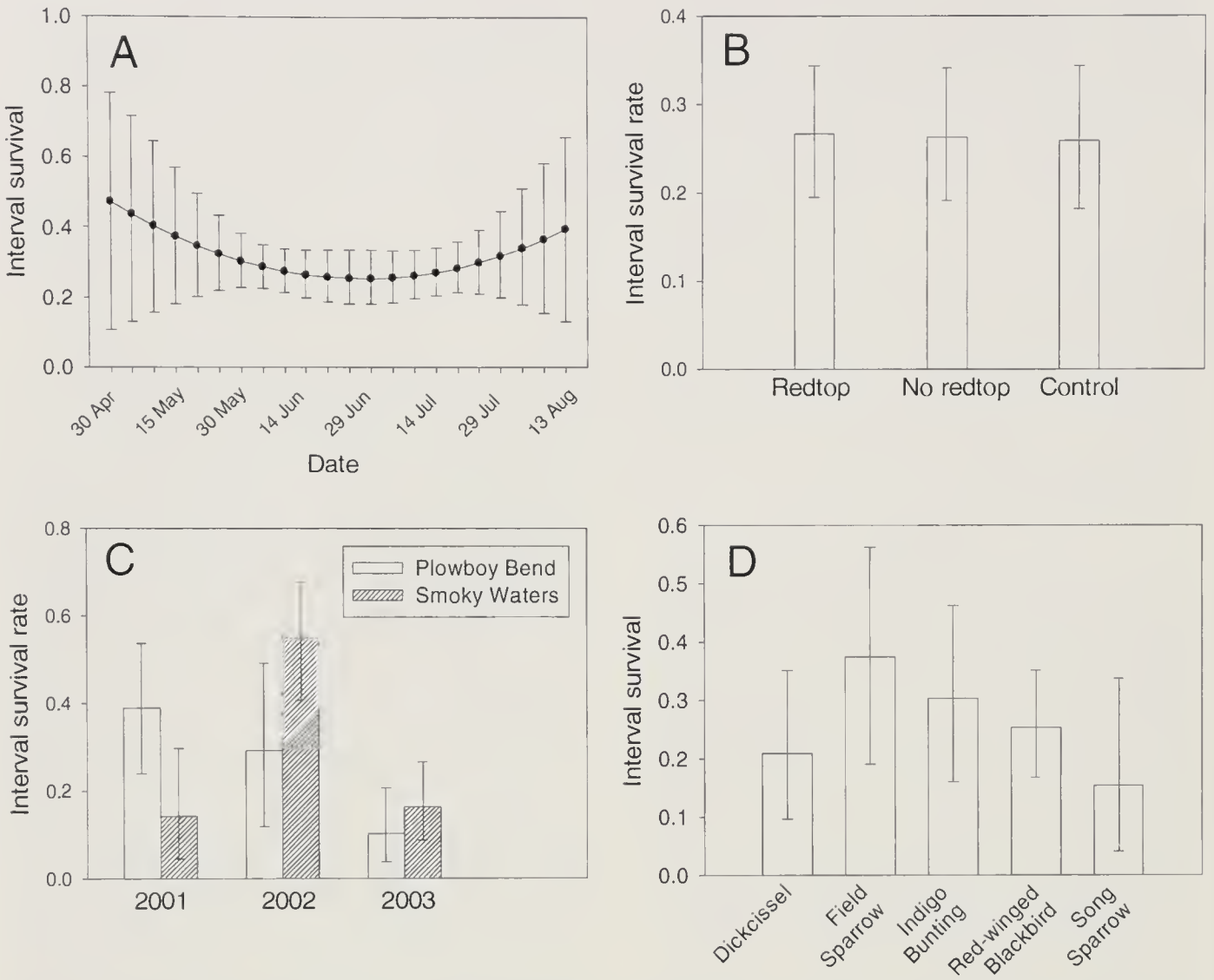

FIG. 1. Model-averaged interval survival estimates (±95% confidence intervals) for covariates (A) day-of-year, (B) restoration treatment, (C) site × year, and (D) species from Missouri River floodplain reforestation sites, 2001–2003.

parasitism frequency was 24.0% for Indigo Buntings (n = 55 nests); other species were rarely parasitized (Dickcissel 5.1%, n = 59 nests; Field Sparrow 4.6%, n = 44 nests; Red-winged Blackbird 0.8%, n = 239 nests; Song Sparrow 3.5%, n = 29 nests). The best-supported model included distance to nearest tree and species (Table 3). Probability of parasitism decreased with distance to the nearest tree (Fig. 2).

Vegetation.—Mean forb cover varied overall among treatments (χ^2 = 13.1, df = 2, $P < 0.05$; Table 4). Mean forb cover was lower in redtop versus no redtop treatments (t = 12.64, df = 2, adj. P = 0.019), but did not differ in pairwise multiple comparisons between other treatments. Grass cover <0.25 m varied overall among treatments (χ^2 = 8.1, df = 2, $P < 0.05$; Table 4) but did not differ in any multiple-comparisons tests between pairs of treatments.

DISCUSSION

We found little support for our principal hypothesis about variability in nest survival due to differences in floodplain restoration treatments. Nest densities generally varied among habitat-treatment types and mean forb cover was lower in redtop treatments; the model relating nest survival to restoration treatment had the weakest support of any model except the null model.

Twedt et al. (2002) working in Mississippi and Louisiana also evaluated songbird nest survival in relation to different floodplain restoration treatments. Their study considered plantings with a wider range of ages (2–10 years) and tree heights (~3–15 m), and they also found no differences in nest survival among treatments. Daily nest survival of Indigo Bunting, Red-winged Blackbird, and Dickcissel in their treatments with nest sample sizes ≥31 ranged from 0.919 to 0.948 (Twedt et al. 2002).

TABLE 3. Candidate models for incidence of cowbird brood parasitism in lower Missouri River floodplains, 2001–2003. Models with a lower ΔAIC and a greater Akaike weight (w_i) have greater support; K is the number of parameters in the model.

Model	K	AIC	ΔAIC	w_i
Distance to nearest tree, species	6	130.89	0.00	0.95
Global, all variables	11	136.88	5.99	0.05
Species only	5	141.96	11.07	0.00
Site, species	6	143.91	13.02	0.00
Year, species	7	144.54	13.65	0.00
Restoration treatment, species	7	145.87	14.98	0.00
Null	1	169.36	38.48	0.00

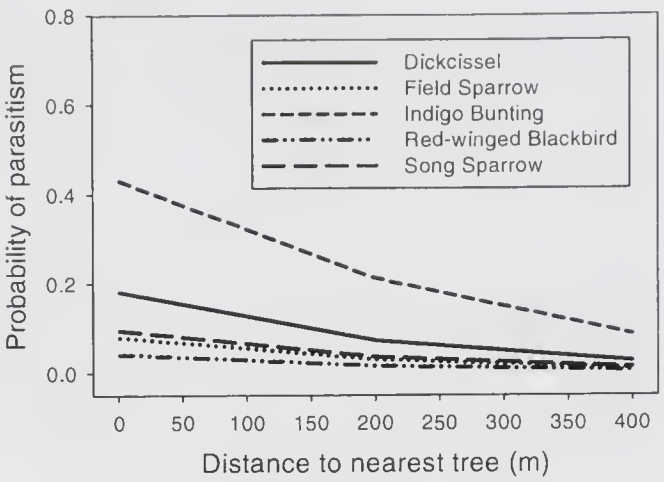

FIG. 2. Model-based probability of cowbird parasitism in relation to distance from nearest tree for songbird species using Missouri River floodplain reforestation sites, 2001–2003.

Daily nest survival rates at our sites were comparable to other studies in central Missouri, but were both higher and lower than sites in northern Missouri. Average daily survival for Field Sparrows in a study at old-field sites <30 km away (Burhans et al. 2002) was 0.936 ± 0.004 (SE) compared with 0.958 from model-based estimates in the present study. Daily nest survival for Indigo Buntings at those same old fields was 0.955 ± 0.003 compared to our model-based estimate of 0.957. In contrast, daily survival of Indigo Buntings nesting in riparian forests and buffer strips in northeastern Missouri was 0.90 (Peak et al. 2004). Our model-based Field Sparrow (0.330) and Dickcissel (0.203) interval survival rates (Fig. 1D) were lower than Mayfield success rates for Field Sparrows (0.472 ± 0.6 SE) and Dickcissels (0.297 ± 0.2) in Conservation Reserve Program sites in northern Missouri (McCoy et al. 1999).

A negative relationship between cowbird parasitism and nest survival was evident from the best model (Table 2), although only four complete nest losses, via nest abandonment, were directly attributable to cowbird parasitism. Nest abandonment attributed to cowbird parasitism has been noted frequently for Field Sparrows at more heavily-parasitized locations (Strausberger and Burhans 2001), but has rarely been documented for Indigo Buntings after clutch initiation (reviewed in Burhans et al. 2000). We may have incorrectly attributed bunting abandonments that were due to death of parents or other disturbances to cowbird parasitism. That would not affect the outcome of the logistic-exposure survival analysis, however, because these nests would still be categorized as parasitized. Parasitized nests could have experienced lower survival if predators were attracted to them because of more frequent and louder begging calls by cowbird offspring (Dearborn 1999) or more frequent visits by host parents (Dearborn et al. 1998). However, we had few parasitized nests that survived sufficiently long to contain cowbird nestlings. A final explanation could be that both nest predators and cowbirds tended to find the same nests.

Considerable variation in nest survival among years, sites, and dates was obvious from our most-supported models of daily survival. Nest survival in an earlier study of Field Sparrow and Indigo Bunting in Missouri old-field habitats (Burhans et al. 2002) was similarly higher in early May and August and lower in June and early July. Temporal patterns in nest survival likely reflect unmeasured variables such as within-season differences in predator activity or among-year differences in predator foraging patterns or abundance. Flooding may have contributed to important yearly mortality differences, particularly at one site. Sixteen nests were lost to flooding at Smoky Waters in 2001 and 2002 with 15 of those lost in 2001, whereas only two nests were lost to flooding at Plowboy Bend, both in 2001 (Fig. 1C). We did not detect a strong effect of nest height on nesting success, although two other studies from the same region found nest survival increased with increasing nest height (Burhans et al. 2002, Burhans and Thompson 2006). The model-averaged parameter estimate for nest height (0.03, CI = −0.10–0.15) suggested a weak positive effect, but the range of heights in the present study (0–2.10 m) was lower (0 to 5.5 and

TABLE 4. Least-squares means (±95% CI) for vegetation measurements from bottomland restoration sites in lower Missouri River floodplains, 2002. Vegetation variables (expressed as proportions), except for mean grass height, are mean cover values across four vertical board measurements taken for each sample.[a]

Vegetation variable	Restoration treatment		
	Redtop	No redtop	Control
Mean grass cover	0.21 ± 0.16	0.16 ± 0.16	0.26 ± 0.16
Mean forb cover	0.05 ± 0.10	0.27 ± 0.10	0.16 ± 0.10
Mean total vegetation	0.27 ± 0.22	0.43 ± 0.22	0.42 ± 0.22
Mean grass height, m	0.80 ± 0.40	0.67 ± 0.40	1.07 ± 0.40
Grass cover <0.25 m	0.81 ± 0.29	0.23 ± 0.29	0.43 ± 0.29

[a] Sixty-eight samples were taken for each treatment in each site.

0 to 3.6 m, respectively). The reduced range of nest heights in our study may not have been sufficient to reveal an effect, given the positive influence of extraordinarily tall nests on survival in Burhans et al. (2002).

Probability of cowbird parasitism decreased with distance to the nearest tree (Fig. 2). This finding is in agreement with those of Clotfelter (1998), Hauber and Russo (2000), and Saunders et al. (2003). Johnson and Temple (1990) found that parasitism frequencies in open prairie habitats were higher near wooded edges, which presumably contained trees for perches, than far from wooded edges. Twedt et al. (2002) found higher parasitism frequencies in stands with tall cottonwood (*Populus* spp.) trees compared to younger stands with shorter trees in Mississippi and Louisiana floodplain restoration sites.

Our sites experienced low parasitism compared to more forested (~70%) sites in the region (Burhans et al. 2000, Burhans and Thompson 2006) despite having low (~33%) landscape-level forest cover. Field Sparrows experienced parasitism of 11.3% (n = 443 nests) in a study of cowbird parasitism in old fields within 30 km of our sites (Burhans and Thompson 2006) compared to 4.6% in this study; Indigo Buntings experienced parasitism frequencies of 48% (n = 295 nests) in old fields compared to 23.6% in this study. Dickcissels were parasitized at 9.6% (n = 242 nests; Winter 1999) in southwestern Missouri prairie fragments compared to 5.1% at our sites; Dickcissels at other sites in the Midwest have been parasitized at frequencies of 60–85% (Zimmerman 1983). Landscapes with low forest cover such as ours are usually associated with high cowbird abundance and parasitism (Robinson et al. 1995, Donovan et al. 2000, Thompson et al. 2000). We observed Brown-headed Cowbirds only rarely during 5 years of breeding point counts at these sites (D. E. Burhans and B. G. Root, unpubl. data), whereas cowbird detections were an order of magnitude higher on point counts at old field sites 30 km distant during the same period (Burhans and Thompson 2006). Old fields and large river floodplains are different habitats, and may be prone to different levels of parasitism (Robinson and Herkert 1997), possibly because of differences in vegetation structure. Twedt et al. (2002) similarly worked at sites having low landscape-level forest cover (36%), but noted lower cowbird numbers in stands having short trees at their restoration sites. Cowbirds could be abundant in these large river landscapes, but possibly select habitats within them that have more or taller trees (Twedt et al. 2002). Studies have shown that regional and landscape effects such as forest cover constrain parasitism at more-local scales (Donovan et al. 2000, Thompson et al. 2000). However, most landscape-level studies have used forested habitats to document parasitism frequencies and cowbird numbers (e.g., Robinson et al. 1995). Several studies have looked at variation in cowbird numbers and parasitism among habitats (Hahn and Hatfield 1995, Strausberger and Ashley 1997, Robinson et al. 1999), but the relationship between landscape-level cowbird abundance and allocation of cowbirds among habitats deserves further work. Much of our understanding about landscape determinants of cowbird parasitism comes from work in the 1980s–2000s in upland forested habitats (Brittingham and Temple 1983, Robinson et al. 1995, Donovan et al. 2000, Thompson et al. 2000). Birds using forested bottomlands, abandoned bottomland fields, and grasslands within large

floodplain agricultural landscapes may differ from forests in habitat preference by cowbirds, and require different management considerations.

We do not have data for livestock presence, but low parasitism in our study could be explained by the apparent scarcity of cattle operations in proximity to our sites. Nesting studies have shown decreases in parasitism with distance from grazed habitats (Goguen and Matthews 1999, 2000) despite cowbirds' ability to commute between breeding and feeding areas (Thompson 1994).

We found differences in habitat use by the species in the restoration treatments, but our data did not show that nest survival varied with planting treatment. Our findings and those of Twedt et al. (2002), who also studied agricultural floodplains low in regional forest cover, indicate that further study of interactions between landscape- and habitat-level patterns in Brown-headed Cowbird abundance and parasitism frequencies are warranted.

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CAROTENOID-BASED MALE PLUMAGE PREDICTS PARENTAL INVESTMENT IN THE AMERICAN REDSTART

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ABSTRACT.—We examined whether male plumage coloration signals parental quality in the American Redstart (*Setophaga ruticilla*), a highly ornamented, migratory warbler. We measured the relationship between both adult male arrival date and phenotype (morphology, melanin- and carotenoid-based plumage), and parental care levels of both parents. Males with brighter flank feathers made more visits to the nest and spent more time at the nest, consistent with the 'good-parent hypothesis'. Female parental care (number of visits) was negatively correlated with intensity of red of her mate's tail feathers and positively associated with her mate's parental effort. These data indicate offspring of brighter males receive more care from both parents. Our results suggest carotenoid-based plumage traits of male American Redstarts may have an important role in intersexual signaling, and add to our understanding of the evolution of multiple ornaments. *Received 10 July 2009. Accepted 20 January 2010.*

Three major models have been developed to explain patterns of association between male ornamentation and parental care. The 'good-parent' hypothesis predicts that when paternal care influences offspring viability directly, males should signal their ability to provide for offspring to prospective mates, and more attractive males should provide more care (Heywood 1989, Hoelzer 1989, Norris 1990, Hill 1999, Siefferman and Hill 2003). Some evidence suggests female parental care does not decrease in response to increased care by their mate, resulting in a net benefit to the offspring of 'good-parent' males (Sanz et al. 2000, Schwagmeyer and Mock 2003, but see Wright and Cuthill 1989, 1990; Markman et al. 1995). Alternatively, the 'differential allocation' hypothesis predicts females mated to more attractive males increase their own level of parental effort to avoid desertion by their mates and to enhance their fitness through production of high-quality offspring (Burley 1986, 1988; Studd and Robertson 1988; Badyaev and Hill 2002). In this model, attractive males restrict their parental investment to allocate more energy towards their own survival, resulting in a negative relationship between male attractiveness and care (Burley 1986, 1988; Møller and Thornhill 1998). A third alternative, the 'trade-off hypothesis', similarly proposes that attractive males provide less care towards their offspring (to be able to seek extra mating opportunities), resulting in a negative relationship between male attractiveness and level of care (Williams 1966, Magrath and Komdeur 2003, Mitchell et al. 2007). Several studies have failed to find a relationship between male plumage and parental care (Rohde et al. 1999, Smiseth et al. 2001, Cooper and Ritchison 2005). Some of these studies, however, involve species with multiple ornaments whose signal function and context are not well understood.

The American Redstart (*Setophaga ruticilla*), a small (7–8 g) neotropical migratory warbler, is particularly suited for studies of male plumage coloration and parental care. American Redstarts are sexually dichromatic and yearling males exhibit delayed plumage maturation, suggesting strong sexual selection on plumage coloration. Adult males are black with bright orange plumage patches on their wings, tail, and sides of the breast (flanks), and a white or black breast, depending on bib size (Sherry and Holmes 1997). The plumage of adult male American Redstarts is highly variable, both in bib size (melanin-based plumage) and orange (carotenoid) coloration (Lemon et al. 1992, Kappes et al. 2009, Reudink et al. 2009b). Recent evidence suggests tail feathers of American Redstarts have an important role in intrasexual signaling during the non-breeding season, where males with brighter tails occupy higher quality winter territories (Reudink et al. 2009a). Additionally, both bib size (Perreault et al. 1997) and flank redness have been linked to a male's ability to secure paternity at his nest during

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the breeding season, and tail brightness to a male's chances of achieving polygyny (Reudink et al. 2009b). In particular, flank feathers may function as a sexual signal in American Redstarts, as males will puff out their breast and flank feathers in a "fluff display" during courtship (Sherry and Holmes 1997).

Our objectives were to quantify variation in plumage ornamentation, morphology, and arrival behavior of adult male American Redstarts, and levels of parental care provided by both parents to offspring to identify which features may provide a reliable signal to females of male parental effort in this highly ornamented songbird. We predicted male plumage coloration would correlate with levels of parental care, based on recent evidence suggesting that different plumage regions may be used to signal information in different contexts (Reudink et al. 2009a, b; Kappes et al. 2009); however, we made no *a priori* predictions as to which plumage region(s) might be important.

METHODS

Field Data and Feather Collection.—We conducted field work at the Queen's University Biological Station in southeastern Ontario, Canada (44° 34′ N, 76° 19′ W), during two consecutive breeding seasons (May–Jul 2006–2007). The 60-ha study site is a mixed deciduous forest, largely dominated by sugar maple (*Acer sacchurum*) and eastern hop-hornbeam (*Ostrya virginiana*). We surveyed transects from 0600 to 1200 hrs EST each day from 1 May to 1 July across the study site to record the arrival date for each individual. We designated arrival date as the number of days after the arrival of the first male each season (i.e., first date of male arrival = 0; male that arrived 5 days later = 5) to standardize arrival date across seasons. We captured adult male redstarts on their respective territories using mist nests and song playback, usually within 7 days of arrival, and females during the nesting phase using mist nets near their nest location. All birds were banded with a Canadian Wildlife Service aluminum band (permit # 10766C) and a unique combination of three color bands (excluding red and orange in males); we recorded unflattened wing chord length (±1.0 mm) as a measure of relative body size. We plucked a single tail feather (third rectrix; R3) and 12–15 orange flank feathers from each male (Quesada and Senar 2006) (CWS collection permit # CA 0154). We classified adult male bib size using a 1–5 scale (1 = small amount of black plumage, 5 = large amount of black plumage with intermediates given half points) following Lemon et al. (1992).

Parental Care Observations.—We monitored American Redstart pairs each season (~40 pairs/season) daily until their nest was found, and observed nests every 1–2 days following completion of nest-building until hatching and recorded the number of young. We confirmed the number of nestlings again on day 5 after hatching and continued to monitor nests until fledging. Fifty nests were observed: 25 in 2006 and 25 in 2007. We erected ground-based video cameras (Canon ZR500) on tripods >5 m from the base of the nest tree on days 5 and 7 after hatching to record parental effort. Cameras were focused on the nest and its immediate (<20 cm) surroundings, and recording occurred between 0600 and 0900 hrs EST. Each recording lasted 120 min and the first 5 min were discarded to allow parents time to recover from human disturbance. The remaining 115 min were used to calculate provisioning rates of males and females, and the time each parent spent at the nest. We recorded and analyzed a total of 148 hrs of video from 38 nests (n reduced due to high predation rates). A trained observer recorded the measures of parental care through binoculars at a distance >10 m from the nest using a stopwatch if there were more nests to be watched than cameras available (2006—day 5: $n = 8$, day 7: $n = 5$; 2007—day 5: $n = 2$, day 7: $n = 2$). There was no difference between video camera and trained observer nest watches in either the number of visits to the nest, or total time at the nest (2-sample t-test assuming unequal variance, all P values > 0.09). Nests depredated between days 5 and 7 were excluded from analysis (2006: $n = 7$; 2007: $n = 5$).

We recorded both the total (i.e., sum of days 5 and 7) number of visits to the nest and the total nest attendance (in sec) for males and females as measures of parental care. Both variables are effective measures of parental effort in small insectivorous birds that make frequent trips to the nest (Saetre et al. 1995). Total time at the nest for males may include activities such as vigilance and removal of fecal sacs, but does not necessarily represent a direct benefit to rearing of offspring as it would for females (i.e., brooding); trips to the nest may serve as a more accurate representation of care, as males are continually bringing food. We divided both total number of visits per hour

and total nest attendance per hour by the number of chicks present in the nest to standardize for brood size and recording time. We compared standardized parental care variables with raw data to ensure that parental effort/hr/chick was representative of total parental effort (linear regressions, all $P < 0.0004$). Six males in our study were polygynous; however, primary and secondary nests were temporally separated, and we included only data from the primary nest (during the period when the male was caring exclusively for the first nest). All individuals were identifiable via color bands, and we were able to ensure that our data set contained no pair duplications across both years.

Color Analysis.—We mounted feathers from each male on black paper (Colorline Ebony #142), and stacked flank feathers as they would naturally lie on the bird (Siefferman and Hill 2003, Quesada and Senar 2006). Mounting feathers on a black background is a standard technique (Siefferman and Hill 2003, Quesada and Senar 2006), and the paper used had low (<5%) reflectance, indicating it would have a minimal impact on our analysis. We omitted samples from further analysis ($n = 5$) in instances where there were too few flank feathers or the orange area on the tail feather was too small to obtain reliable readings. We analyzed male plumage and parental care observations for both males and females from 16 nests in 2006 and 17 nests in 2007.

We gathered reflectance spectra from flank and tail feathers of each male using a PX-2 pulsed xenon light source attached to an Ocean Optics USB2000 spectrometer (Dunedin, FL, USA). We took 25 readings throughout the orange (carotenoid-based) region for both flank and tail feathers following Reudink et al (2009b). We gathered raw reflectance data into 10 nm bins from 320 to 700 nm using CLR1.0.3 (Montgomeric 2008), and averaged across the 25 measurements. We calculated brightness for tail and flank feathers by averaging percent reflectance from 320 to 700 nm (color variable 1: 'brightness'). The carotenoid-based plumage of American Redstarts consists of peaks in both the UV and red/orange regions of the spectrum. We used principal component analysis (PCA) to collapse the spectrum into a smaller set of independent variables that describe the measures of hue and chroma based on shape of the curve while controlling for variation in brightness (Cuthill et al. 1999, Montgomerie 2006, Stein and Uy 2006, Reudink et al. 2009b). We verified this method by calculating hue and chroma using the equations: hue=arctan ($[R_{415-510} - R_{320-415})/R_{320-700}]/[R_{575-700} - R_{415-575})/R_{320-700}]$), UV chroma = $R_{320-415}/R_{320-700}$, and red chroma = $R_{575-700}/R_{320-700}$.

Flank PC I described 85.5% of the variation in shape of the reflectance curve, and loaded positively on short (UV) wavelengths and negatively on the longer (red/orange) wavelength region of the spectrum. Flank PC I associated negatively with both hue ($r^2 = 0.68$, $n = 32$, $P < 0.001$) and red chroma ($r^2 = 0.99$, $n = 32$, $P < 0.001$), and associated positively with UV chroma ($r^2 = 0.81$, $n = 32$, $P < 0.001$). Tail feather PC I explained 48.4% of the variation, and loaded positively on both the shorter and longer wavelength regions of the spectrum, and negatively on intermediate wavelengths. Tail PC I associated positively with hue ($r^2 = 0.16$, $n = 33$, $P = 0.02$) and red chroma ($r^2 = 0.61$, $n = 33$, $P < 0.001$), but had no association with UV chroma ($r^2 < 0.001$, $n = 33$, $P = 0.94$). The first principal component from both plumage regions was used to describe 'redness' (color variable 2 = 'redness'), where birds with greater 'redness' have more negative flank PC I values, and more positive tail PC I values.

Statistical Analysis.—All statistics were performed using JMP 7.0 (SAS Institute 2007) and R 2.6.1 for Windows (R Development Core Team 2007). We pooled data across both years of study and, in instances where data for the same individual were collected across 2 years ($n = 3$), avoided pseudoreplication by randomly selecting 1 year to exclude. We used paired *t*-tests to compare the parental care variables across both observation days (for both males and females), as well as across gender, and linear regression to examine the relationship between a pair's number of visits to the nest, and total nest attendance. All plumage variables were tested for co-linearity using Pearson's pairwise analysis. We applied backwards stepwise multiple regressions with parental care variables (male visits/hr/chick, female visits/hr/chick, male time at the nest/hr/chick, female time at the nest/hr/chick) as the response variable to calculate the factors that best predicted both male and female parental care. We used measures of male tail brightness, tail redness (PC I), flank brightness, flank redness (PC I), bib score, body size, year, and arrival date as our main effects in each model.

RESULTS

Male American Redstarts did not show a difference in mean time (sec ± SD) spent at the nest between days 5 (108.21 ± 112.53) and 7 (77.98 ± 75.66) (paired *t*-test, $t_{32} = 1.65$, $P = 0.11$); however, mean number of visits for males on day 7 (1.92 ± 0.73) after hatching were greater than on day 5 (1.52 ± 0.81) (paired *t*-test, $t_{32} = -2.89$, $P = 0.007$). Females showed no difference in the mean number of visits to the nest between days 5 (1.56 ± 0.59) and 7 (1.72 ± 0.68) (paired *t*-test, $t_{32} = -1.78$, $P = 0.09$), but spent significantly more time at the nest on day 5 (778.04 ± 484.18 sec) than day 7 (616.68 ± 523.90 sec) (paired *t*-test, $t_{32} = 3.54$, $P = 0.001$). Females did not visit the nest more or less frequently than males (paired *t*-test, $t_{32} = 1.27$, $P = 0.21$), but did spend a greater amount of time at the nest (paired *t*-test, $t_{34} = -7.91$, $P < 0.0001$). There was a significant positive relationship between each member of a breeding pair for number of visits ($r^2 = 0.21$, $F_{1,31} = 8.17$, $P = 0.008$) and nest attendance ($r^2 = 0.30$, $F_{1,31} = 13.11$, $P = 0.001$).

Pairwise correlations between all male plumage variables revealed that tail brightness increased with decreasing tail redness (PC I) ($r^2 = 0.12$, $F_{1,31} = 4.30$, $P = 0.05$). No other plumage variables were significantly correlated.

Plumage Color and Provisioning.—Results of a backwards stepwise multiple regression revealed total number of male visits/hr/chick was significantly predicted by the brightness of flank feathers (Table 1). This data set contains one high value for flank brightness (Fig. 1). This point is not due to a technical error in measurement, as readings taken before and after this point were within the normal range, and this point remained high after repeated measurements. This individual was also within the normal range for all other measures. The correlation between male flank brightness and number of visits/hr/chick remained significant when this point was excluded (Fig. 1). Flank brightness was also a significant predictor of total time spent by males at the nest (Table 1). Female visits were significantly predicted by year and mate's tail redness (Table 1), where females in 2007 made more trips to the nest than those in 2006 (two-sample *t*-test assuming unequal variance, $t_{25} = -2.77$, $P = 0.01$). There was a negative relationship between female visits to the nest and male tail redness, where females which made fewer trips to the nest were paired to males with redder tails (Fig. 2). None of the remaining variables related to arrival date, morphology, or plumage predicted male or female levels of parental care.

DISCUSSION

The brightness of flank feathers in adult male American Redstarts predicted their total number of visits to the nest, and total time spent at the nest. Our results are consistent with the 'good-parent' hypothesis and suggest that flank feather brightness may provide a reliable signal of parental effort in adult male American Redstarts. A significant negative correlation was found between number of female visits to the nest and redness of her mate's tail feathers. We found a strong positive correlation between breeding partners for visits to the nest, and nest attendance.

The 'good-parent' hypothesis predicts that attractive males should signal their ability to provide increased levels of parental care, compared to less attractive males (Heywood 1989, Hoelzer 1989). We show brightness of male carotenoid-based flank plumage is associated with levels of male parental care. Plumage brightness has been found to predict mating success in other species, such as Golden-collared Manakins (*Manacus vitellinus*) (Stein and Uy 2006). In addition, it has been linked to stronger immune response to novel antigens (Saks et al. 2003a), suggesting it has an important role in signaling male health status and, potentially, the ability to provide for offspring.

The pairwise correlation analysis among all male plumage variables revealed only one significant association; tail brightness increased with decreasing tail redness. This suggests that in American Redstarts, plumage brightness does not necessarily correspond to greater feather carotenoid content (Saks et al. 2003b, Andersson and Prager 2006). Instead, plumage brightness may be influenced by the underlying structural matrix of feathers (Shawkey and Hill 2005); several studies have linked structural-based colors with condition/individual quality (Doucet 2002, Doucet and Montgomerie 2003) as well as the level of male parental care (Siefferman and Hill 2003). However, the interactions between structural and pigment-based components of feather coloration remain poorly understood and further research is needed to elucidate patterns of plumage brightness.

Recent work by Kappes et al. (2009) with a smaller sample of more southerly breeding

TABLE 1. Multiple regression models examining male and female parental care variables in relation to standardized arrival date, wing length, bib score, flank feather brightness and redness, and tail feather brightness and redness. Initial models are shown for each model. Final models (i.e., models following removal of nonsignificant effects by stepwise backward deletion) are also shown where predictor variables were significant. Sample size increased in the final models where removal of nonsignificant predictor variables added additional individuals to the model that were missing information for these variables.

	Predictor variables	β	F	P
Male visits/hr/chick (initial model, $n = 31$, $r^2 = 0.46$)	Year	0.13	0.09	0.77
	Standardized arrival	0.01	0.26	0.62
	Wing	0.06	0.51	0.48
	Bib score	0.06	0.15	0.70
	Flank brightness	0.12	3.91	0.06
	Flank redness (PC I)	0.03	0.92	0.35
	Tail brightness	−0.03	0.12	0.74
	Tail redness (PC 1)	−0.04	1.37	0.25
Male visits/hr/chick (final model, $n = 32$, $r^2 = 0.37$)	Flank brightness	0.11	15.004	**0.0006**
Male visits/hr/chick (initial model, $n = 31$, $r^2 = 0.19$)	Year	22.45	0.18	0.68
	Standardized arrival	1.34	0.20	0.66
	Wing	1.50	0.03	0.88
	Bib score	−6.74	0.14	0.71
	Flank brightness	4.81	0.52	0.48
	Flank redness (PC I)	3.40	0.84	0.37
	Tail brightness	1.31	0.02	0.89
	Tail redness (PC I)	−2.19	0.24	0.63
Male visits/hr/chick (final model, $n = 32$, $r^2 = 0.1$)	Flank brightness	6.39	4.34	**0.05**
Female visits/hr/chick (initial model, $n = 31$, $r^2 = 0.42$)	Year	0.69	4.15	0.05
	Standardized arrival	−0.02	0.69	0.42
	Wing	0.02	0.10	0.76
	Bib score	0.06	0.30	0.59
	Flank brightness	−0.02	0.17	0.69
	Flank redness (PC 1)	0.004	0.03	0.87
	Tail brightness	0.03	0.19	0.67
	Tail redness (PC I)	−0.05	3.24	0.09
Female visits/hr/chick (final model, $n = 32$, $r^2 = 0.33$)	Year	0.49	9.30	**0.005**
	Tail redness (PC 1)	−0.05	8.16	**0.008**
Female visits/hr/chick (initial model, $n = 31$, $r^2 = 0.14$)	Year	357.2	1.14	0.30
	Standardized arrival	−9.75	0.27	0.61
	Wing	43.61	0.49	0.49
	Bib score	64.12	0.31	0.58
	Flank brightness	−28.60	0.46	0.50
	Flank redness (PC I)	27.75	1.39	0.25
	Tail brightness	61.82	1.11	0.30
	Tail redness (PC I)	−5.15	0.03	0.86
Female visits/hr/chick (final model, $n = 33$)	No significant predictors			

American Redstarts, found males with brighter flanks provisioned less than duller males, and those with less red flanks sired more total young. Flank brightness and tail brightness in our study, in agreement with Kappes et al. (2009), were not related suggesting the two plumage regions may be used as signals in different contexts. Flank redness (PC I) is related to genetic paternity (indicating that it may act as a measure of genetic quality) (Reudink et al. 2009b), and our results suggest that flank brightness may also act as an intersexual signal of parental care.

Recent evidence suggests American Redstart tail feather coloration acts as an intrasexual signal. Specifically, tail brightness is related to both territory quality in wintering areas (Reudink et al.

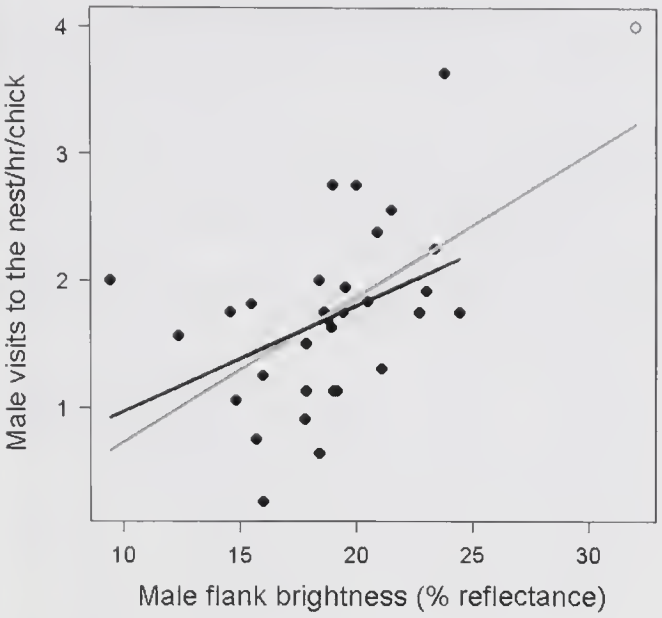

FIG. 1. Linear regression of male visits to the nest (standardized/hr/chick) on flank feather brightness. Gray regression line ($r^2 = 0.34$, $F_{1,30} = 15.29$, $P = 0.0005$) includes high value (open circle). Black regression line ($r^2 = 0.16$, $F_{1,29} = 5.66$, $P = 0.02$) excludes this individual.

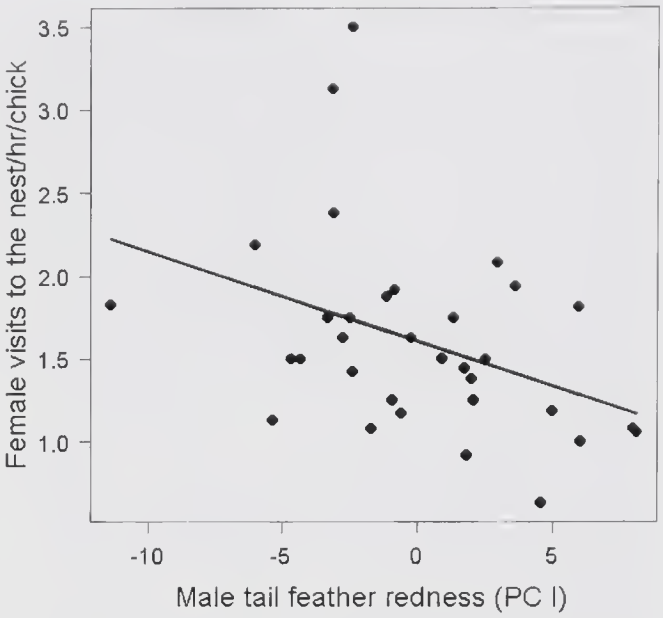

FIG. 2. Linear regression of female visits to the nest (standardized/hr/chick) on tail feather redness (PC I) ($r^2 = 0.15$, $F_{1,31} = 5.60$, $P = 0.02$). X-axis values are from low to high, where individuals with more negative score (e.g., −10) have tails with lower redness than those with higher values.

2009a) and polyterritorial polygyny in breeding areas (Reudink et al. 2009b). We found no relationship between tail brightness and either male or female parental care; however, female visits to the nest were negatively correlated with the redness of male tail feathers. Plumage redness is often associated with greater carotenoid deposition into the feather structure; high quality birds would be assumed to have redder feathers (Saks et al. 2003b). However, the redness of American Redstart tail feathers has been found to significantly decrease across subsequent breeding seasons (Reudink et al. 2009b). One suggestion is that female American Redstarts alter their level of parental care based on the perceived age of their mates with females providing more care when paired with older males, although we do not currently have the data to address this possibility.

Neither male bib size nor arrival date was correlated with any measure of parental care by males or females. Consistent with previous studies (Perreault et al. 1997, Reudink et al. 2009b, but see Lemon et al. 1992), bib size does not appear to have a prominent signaling role; however, arrival date has previously been shown to be an important predictor of reproductive success (Norris et al. 2004, Reudink et al. 2009c). Reudink et al. (2009c) demonstrated that early arriving males were more likely to achieve polygyny than those which arrived at a later date. However, when males occupy multiple territories and provide care for multiple nests, there may be a limit to the amount of care one male can provide, as evidenced by male American Redstarts providing relatively less care at their second nest, than at their primary nest (Secunda and Sherry 1991; RRG, unpubl. data).

The strong relationship between both female and male visits to the nest, and nest attendance suggests that offspring of more ornamented males are receiving the benefit of more care by both parents. Our results also suggest the potential for assortative mating, where females that provide more care pair with males which do the same. These data conform to models which suggest that equality of investment in species with biparental care is an evolutionarily stable strategy (offspring receive a benefit from both parents providing high amounts of care, reviewed in Wright and Cuthill 1989). Unfortunately, our data do not allow us to differentiate the effects of individual feeding effort from those of territory quality, as both male and female feeding rates could be affected by availability of food on their territory. It is also possible that male coloration is not indicative of parental care, but rather the association arises from brighter males obtaining higher quality territories and provisioning chicks more often with less effort. Male American Redstarts able to secure high quality territories during the overwintering season arrive earlier in breeding areas

and show higher levels of realized reproductive success (Reudink et al. 2009c). One possibility is that socially dominant males arriving earlier from high quality winter territories also obtain higher quality territories during the breeding season, in which case we should observe a relationship between arrival and provisioning. We did not observe a relationship between male arrival date and parental care, but direct measurements of territory quality are needed to discern how variations in individual and territory quality influence provisioning.

The brightness of male American Redstart flank feathers may have an important role in intersexual signaling but further research is needed to clarify female mate choice in this system. Experimental approaches that measure female response to changes in male ornamentation would be most useful. Research on the ornamental qualities of female plumage to examine if females with brighter carotenoid-based plumage provide more for their offspring and pair with brighter males would also be informative.

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VARIATION IN PLUMAGE COLORATION OF NORTHERN CARDINALS IN URBANIZING LANDSCAPES

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ABSTRACT.—Biologists know relatively little of how one of the most important avian phenotypic signals, feather coloration, may be affected by anthropogenic changes resulting from urbanization. We examined the relationship between urbanization and carotenoid-based plumage color of Northern Cardinals (*Cardinalis cardinalis*) in 13 riparian forests distributed across a rural-to-urban landscape gradient in central Ohio, USA. Feathers and morphometric measurements were collected from breeding territorial males (n = 129) and females (n = 145) during March–August 2006–2008. Plumage brightness of males, but not females, increased with body condition (i.e., size-adjusted mass) and declined with amount of urbanization surrounding forests in which cardinals bred. The extent plumage coloration reflected condition was partially mediated by landscape composition. Specifically, the relationship between brightness and body condition was most pronounced in the most rural landscapes. The interdependency of male coloration and body condition may be more relaxed in urban than rural landscapes if carotenoid-rich foods from anthropogenic and/or invasive sources are more available, or are accessible to birds across a wide range of condition. *Received 11 May 2009. Accepted 18 January 2010.*

Most studies of birds in human-dominated landscapes have described striking and relatively predictable patterns in response of species diversity and abundance to intensity of urban development (Blair 1996, Anderies et al. 2007, Devictor et al. 2007, Tratalos et al. 2007). Subtle consequences of urbanization, such as changes in behavior or coloration are less commonly examined. Biologists continue to have a poor understanding of how urbanization might influence plumage coloration, despite a century of interest in causes and consequences of this important phenotypic signal in birds (Andersson 1994, Bortolotti 2006). Most studies of avian coloration in urban systems have focused on detrimental effects of anthropogenic pollution upon levels of carotenoids in plant and animal matter (Sillanpaa et al. 2008) as well as plumage coloration, as in Great Tits (*Parus major*) (Eeva et al. 1998, Isaksson et al. 2005, Isaksson and Andersson 2007). The presence of certain exotic plants, some of which are positively associated with urban development (Borgmann and Rodewald 2005), also can affect coloration by altering access to diet-derived pigments. For example, Mulvihill et al. (1992) showed that access to exotic honeysuckle fruits (*Lonicera* spp.) containing rhodoxanthin, a carotenoid-group (xanthophylls) pigment, changed retrix-tip colors of Cedar Waxwings (*Bombycilla cedrorum*) from yellow to orange. However, the consequences of urbanization affecting avian coloration remain poorly understood despite these studies.

One of the primary ways in which urban development might affect plumage coloration is by altering food resources. Cities generally contain a variety of novel food resources, including bird seed at feeders, fruit from exotic plants, and refuse that can change diets. These changes in food resources can directly affect coloration through increased availability of pigment-containing food sources. The link between diet and plumage coloration should be particularly strong for species that have carotenoid-based plumages, which are highly dependent on carotenoid pigments obtained from food sources (Møller et al. 2000, McGraw et al. 2001, Hill et al. 2002). However, access to pigments is not the sole determinant of coloration because individuals may differ in their ability to use ingested pigments (McGraw and Hill 2001). A variety of urban-associated factors, such as abundant human-commensal predators, oxidative stressors (e.g., pollution), and high avian densities, may constrain the ability of individuals to acquire or physiologically sequester carotenoids for color production (Møller et al. 2000, Isaksson and Andersson 2007). Consequently, plumage quality is known to reflect general health or immunocompetence (Andersson 1994, Saks et al. 2003, Jawor and Breitwisch 2004, Dawson and Bortolotti 2006, Mancy et al. 2008), individual quality (Hill 1991, Kristiansen et al. 2006), and quality of the environment in which birds live (Arriero and

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TABLE 1. Land cover characteristics within a 1-km radius of 13 riparian-forest study sites in urbanizing landscapes in central Ohio, USA

Study site	Urban index	Buildings[a]	Forest width (m)	Proportion of 1-km-radius area covered			
				Agriculture	Lawn	Pavement	Road
Public Hunting	−1.15	210	194	0.32	0.08	0.01	0.01
Prairie Oaks	−1.12	58	148	0.47	0.12	0.03	0.02
Three Creeks	−0.71	92	133	0.10	0.10	0.04	0.02
South Galena	−0.57	185	163	0.14	0.30	0.02	0.01
Galena	−0.48	360	277	0.15	0.22	0.04	0.02
Elk Run	−0.16	812	167	0.31	0.27	0.06	0.05
Woodside Green	0.32	1,227	104	0.11	0.40	0.07	0.05
Rush Run	0.75	1,611	150	0.00	0.41	0.09	0.06
Cherrybottom	0.76	997	165	0.02	0.36	0.16	0.07
Kenny	0.89	1,733	126	0.00	0.34	0.17	0.06
Casto	1.25	1,776	202	0.00	0.42	0.20	0.08
Lou Berliner	1.26	2,272	156	0.00	0.28	0.23	0.08
Tuttle	1.61	2,285	160	0.00	0.34	0.30	0.09

[a] Number of buildings per landscape.

Fargallo 2006). Thus, coloration might be a useful indicator of cryptic detrimental or beneficial effects of urbanization upon an ecosystem.

We used the Northern Cardinal (*Cardinalis cardinalis*) as a model species to examine the extent to which coloration varied with individual body condition and the amount of urbanization surrounding forested parks in central Ohio, USA. The Northern Cardinal is a socially monogamous, dichromatic, year-round resident that exhibits a single annual molt immediately after the breeding season (Halkin and Linville 1999). Cardinals display a brilliant red carotenoid-based plumage that is highly dependent upon their diet (Linville and Breitwisch 1997, McGraw et al. 2001). The species is known to respond positively to urbanization, likely as a consequence of more abundant nesting substrates, fruit resources, bird feeders, and warmer winter temperatures than in comparable rural landscapes (Leston and Rodewald 2006, Rodewald and Bakermans 2006). Previous studies indicate that forests within urban landscapes contain nearly three times the amount of fruit and nearby bird feeders than in rural areas (Atchison and Rodewald 2006, Leston and Rodewald 2006). Increased fruit resources are primarily from the presence of exotic and invasive species, such as Amur honeysuckle (*Lonicera maackii*) and multiflora rose (*Rosa multiflora*). These increased food resources represent one of many ways that urbanization may influence the condition and coloration of cardinals.

Specifically, we asked (1) does plumage coloration vary along a rural-to-urban landscape gradient, and (2) does plumage coloration reflect differences in condition among individuals?

METHODS

Study Sites.—Cardinals were studied at 13 riparian forest sites within the Scioto River Watershed of central Ohio, USA (Table 1, modified from Rodewald and Shustack 2008b). Study sites consisted of mature forest corridors ≥250 m long and ≥100 m wide with all study sites separated by >2 km. Riparian forests across the study area were generally similar in both shape and landscape configuration (i.e., they were narrow, linear, highly-connected forests in fragmented landscapes).

We described the amount of urbanization surrounding each study site using an urban index developed for a larger concurrent study of avian communities across 35 sites (Rodewald and Shustack 2008b). Landscape composition within a 1-km radius of each site was calculated based on digital orthophotographs (2002–2004) and existing data from county auditors. An urban index was calculated for each site to represent the amount of urbanization surrounding that particular forest. Positive values of the urban index indicate increasingly urban forests, which were generally surrounded by >800 buildings within the 1-km radius, and bordered by residential or commercial areas. Negative urban index values represent more rural forests, which were generally surrounded by <360 buildings and bordered by

agricultural fields or pastures (described in Rodewald and Shustack 2008b).

Feather Sampling.—Feather samples were collected from 281 Northern Cardinals captured in mist nets during the breeding season from early March to mid-August 2006–2008. We measured right tarsus length (nearest 0.1 mm), mass (g), and length of the right unflattened right wing chord (nearest 0.5 mm) for all individuals captured. Six to 10 feathers were collected from the breast of each male while 3–6 feathers were collected from the underwing coverts of both wings of females. These areas of feather collection were chosen because they are known to be important areas for cardinal coloration and have been used in previous studies (Linville and Breitwisch 1997; Wolfenbarger 1999a, c; Jawor et al. 2003, 2004). Collected feathers were labeled, stored in manila coin envelopes, and placed in a freezer until measured.

Color Measurements.—Feathers from each individual were superimposed in layers of three on 4.5 × 7.5 cm white note cards to imitate the plumage surface of a bird (Bennett et al. 1997, Quesada and Senar 2006). Superimposed feathers were photographed at a distance of 2 cm using a supra-macro feature of a Fujifilm FinePix S8000fd digital camera. Feathers were photographed inside an 20 × 20 × 20 cm Digital Concepts Lighting Studio (with 2 20-watt lights directed at the feathers) to standardize lighting conditions. Images were imported into Adobe Photoshop CS 2™, a program which quantified hue, saturation, and brightness. Hue was defined as a certain point on the color spectrum and was measured on a circular scale in degrees with 0° (360°) being the purest red color (i.e., red with few blue or yellow tones). The program quantified saturation as a percentage of density with 0% being least dense and 100% being most dense (i.e., least amount of gray tones). Brightness was quantified on a percentage grayscale with 0% being black and 100% being white. The color-picker tool (3 × 3 eye-dropper sample) was used to randomly measure and quantify plumage coloration at 10 points within the largest overlapping area of the superimposed feathers. We examined the precision of our color measurements by repeating them 10 times and calculating the coefficient of variation for measurements for each individual. Within-individual measurements were precise for brightness (CV range = 0.5–4.4; mean ± SE = 1.93 ± 0.04) and saturation (CV range = 0.5–5.7; mean ± SE = 1.82 ± 0.05). Hue measurements showed only small amounts of variation (CV range = 1.8–34.9; mean ± SE = 7.26 ± 0.25). Consequently, the mean of the 10 repeat measurements was used to represent plumage coloration for each individual. Our approach to color quantification is widely used (Kilner 1997, Kilner and Davies 1998, Dale 2000, Gerald et al. 2001, Fitze and Richner 2002, Bortolotti et al. 2003, Bezzerides et al. 2007, Surmaki and Nowakowski 2007), but it does not necessarily reflect how plumage is perceived by other cardinals. Also, this method is not sensitive to UV light as perceived by birds (Cuthill 2006), although previous studies involving carotenoid plumages reported positive correlations among yellow-red spectrum (500–700 nm) and UV reflectance peaks (Senar and Quesada 2006).

Data Analysis.—We reduced the number of color variables by applying a principal components analysis to hue, saturation, and brightness measures separately for males and females. The first two factors for males explained 47% (eigenvalue = 1.40) and 34% (eigenvalue = 1.01) of the variation in plumage color. The first factor (hereafter called "brightness") was strongly correlated with brightness (−0.75) and saturation (0.84), whereas the second factor (hereafter referred to as "hue") was strongly correlated with hue (0.89). Only the first factor was useful for females explaining 55% (eigenvalue = 1.67) of the variation in plumage color. This first factor (hereafter called "hue") loaded positively for hue (0.86) and negatively for saturation (−0.85).

We first developed a condition index to examine relationships between coloration and body condition using principal component analysis (PCA) on wing and tarsus length for males and females separately (SAS Institute 2002). The first factor explained 60% of the variation in body size in males (eigenvalue = 1.19) and was positively correlated with both wing and tarsus (0.77 for each). The first factor for females explained 62% of the variation in body size (eigenvalue = 1.25) and was positively correlated with both wing and tarsus (0.79 for each). We then regressed mass against this body-frame-size factor for 129 males and 145 females. Mass was positively associated with body size for males ($F_{1,127} = 11.92$, $P < 0.001$), and residuals were used as a body condition index, which indicated if individuals were heavier (positive value) or lighter (negative value) than expected for a given body (frame)

size. Variation in female mass was not a function of body size ($F_{1,143} = 20.72$, $P = 0.399$), and we used mass alone to examine condition of females.

We used mixed effects models to test how (1) condition was related to the urban index, year, and urban by year interaction (urban and year treated as fixed effects; site treated as random effect), and (2) how plumage coloration was influenced by condition, the urban index, and a condition by urban interaction (urban and condition treated as fixed effects; site and year treated as random effects). These models were used separately for males and females, and for each of the two principal components describing plumage color. We also considered how plumage variation among individuals might be related to urbanization for males and females, separately, by examining coefficient of variations for color metrics at each site, by male/female, and year. We used a mixed effect model with year as a random effect and the urban index as a fixed effect.

RESULTS

Our derived principal component (lower values indicate brighter plumage) indicated male plumage was brighter as condition improved (condition $\beta = -0.12 \pm 0039$ SE; $F_{1,111} = 10.09$, $P = 0.002$, Fig. 1A), but declined with amount of urban development surrounding forest patches (urban $\beta = 0.17 \pm 0.079$ SE; $F_{1,111} = 4.92$, $P = 0.029$, Fig. 1B). We detected a significant condition by urbanization interaction ($\beta = 0.10 \pm 0.036$ SE; $F_{1,111} = 7.77$, $P = 0.006$, Fig. 2), indicating the relationship between brightness and condition was stronger in rural than urban landscapes. Condition varied among years (parameter estimates were -1.99 ± 0.479 SE for 2006, -1.44 ± 0.479 SE for 2007 with 2008 as the reference year; $F_{1,111} = 9.54$, $P < 0.001$), but was not directly related to the urban index ($F_{1,111} = 1.76$, $P = 0.1869$) nor via an urbanization by year interaction ($F_{1,111} = 0.22$, $P = 0.8025$). Hue was not significantly related to either condition ($F_{1,111} = 0.49$, $P = 0.3484$) or urbanization ($F_{1,111} = 0.06$, $P = 0.800$), nor was there a condition by urbanization interaction ($F_{1,111} = 0.79$, $P = 0.376$). We found no evidence that among-individual variation of male coloration at sites changed along the rural-urban gradient for either brightness ($F_{1,28} = 0.01$, $P = 0.917$) or hue ($F_{1,28} = 0.54$, $P = 0.467$).

We found no evidence that plumage coloration of females was related to mass ($F_{1,127} = 0.50$, $P = 0.480$), urbanization ($F_{1,127} = 0.28$, $P = 0.597$), or a mass by urbanization interaction ($F_{1,127} = 0.22$, $P = 0.638$). Variation in coloration among females was not significantly related to urbanization ($F_{1,29} = 1.19$, $P = 0.284$). We found some evidence that mass varied with urbanization in some years (urban by year interaction estimates: -1.47 ± 0.75 SE for 2006; 0.60 ± 0.808 SE for 2007 with 2008 as the reference year; $F_{1,127} = 3.60$, $P = 0.0301$), but mass was not directly related to either urbanization ($F_{1,127} = 2.19$, $P = 0.1416$) or year ($F_{1,127} = 1.04$, $P = 0.3568$). Female mass declined with urbanization in 2006, but showed no pattern in 2007 and 2008.

DISCUSSION

Brightness of male plumage increased with body condition, but declined as the amount of urbanization surrounding forests in which cardinals bred increased. The relationship between brightness and body condition was stronger in more rural than urban landscapes. The interdependency of coloration and body condition may be relaxed in urban landscapes if birds in comparatively poor condition have access to carotenoid-rich foods due to supplemental feeding or fruits of exotic shrubs. We know in our study system that urban development promotes invasion by exotic Amur honeysuckle (Borgmann and Rodewald 2005), which also is the largest source of fruit at our sites (Leston and Rodewald 2006). Mulvihill et al. (1992) reported that access to exotic honeysuckle fruits containing rhodoxanthin, a carotenoid-group (xanthophylls) pigment was responsible for orange, rather than yellow, tipped retrices of Cedar Waxwings. The weaker interdependency of condition and coloration in urban landscapes may explain why we failed to find a direct relationship between male condition and urbanization, despite the reduced brightness of urban males.

Others have identified links between plumage and individual quality (Linville et al. 1998, Wolfenbarger 1999b, Jawor and Breitwisch 2004), but we found the extent plumage coloration reflected condition was partially mediated by landscape composition. Our findings suggest plumage coloration may prove to be a less useful indicator of male quality in urban landscapes. The potential decoupling of coloration and quality

FIG. 1. Relationship of plumage brightness as described by the first principal component to (A) body condition and (B) urban index of 129 male Northern Cardinals in riparian forests of central Ohio, 2006–2008.

may have important consequences given that coloration can serve as a useful cue in mate selection (e.g., sexual selection; Darwin 1871, Andersson 1994) and, in the case of cardinals, is known to promote assortative mating (Jawor et al. 2003).

Our finding that among-individual variation in plumage was not related to urbanization provides insight into the assertion that synanthropic birds may overmatch resources in urban environments (Shochat 2004). Studies have shown that when individuals have more access or are less limited in sequestering carotenoid resources, they converge on a similar plumage display, resulting in less variation among individuals (Hill 1992). The comparatively dull plumage of urban birds suggests that densities may exceed resource levels. However, in the case of overmatching, one also would expect to find high variation among individuals in coloration, as only a few birds would have access to the best resources. Carotenoids are generally considered to be a limiting resource among birds displaying carotenoid-based plumages (Møller et al. 2000, Dale 2006), specifically for Northern Cardinals (Linville and Breitwisch 1997). One would expect increased intraspecific competition would constrain individual access to carotenoids in areas where carotenoids are especially limited due either to environmental gradients or density-

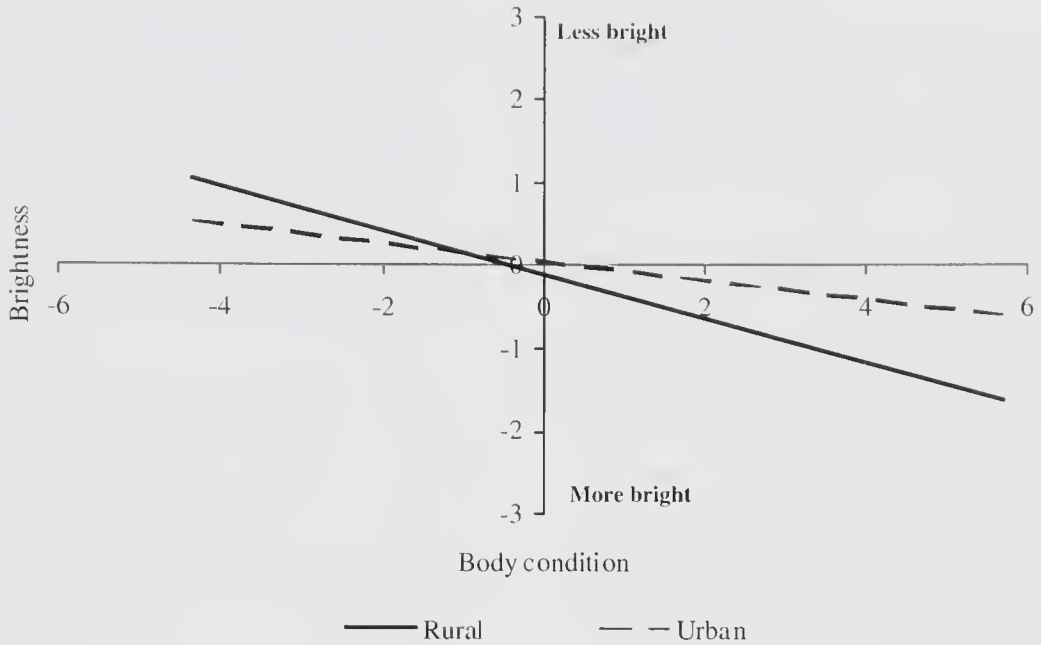

FIG. 2. The relationship between body condition and plumage brightness (i.e., principal component I) was stronger for rural (n = 42) than urban (n = 86) male cardinals breeding in riparian forests of central Ohio, 2006–2008.

dependence, thereby increasing variation in plumage coloration among individuals. High variation in carotenoid-based coloration among individuals might be an indicator of the availability of reduced carotenoids in a particular environment. We found no evidence of greater variation in access to carotenoids than individuals in more rural forests despite greater densities of breeding pairs in urban landscapes (Leston and Rodewald 2006, Rodewald and Bakermans 2006). Supplemental food resources associated with residential land, such as bird feeders and fruiting plants (Atchison and Rodewald 2006, Leston and Rodewald 2006) may permit high densities of cardinals to use similar or greater per capita food resources than birds living in more rural environments. This scenario of apparent resource-matching is consistent with patterns reported by Rodewald and Shustack (2008a), which showed that survival, reproductive productivity, and energetic condition of cardinals were similar across the rural-to-urban gradient.

The presence of a relationship between coloration and urbanization suggests development surrounding forests influences the ability of cardinals to either acquire or sequester carotenoid pigments. However, there are a number of important caveats to our findings. First, given that coloration of cardinals may improve with age (Wolfenbarger 1996), we cannot exclude the possibility that different age structure in urban and rural populations contributed to the observed patterns. Second, there is a possibility that cardinals molted and grew feathers at different locations than where they were captured, which may reflect different food conditions. However, cardinals in the study system: (1) established breeding territories beginning in March, (2) generally molted in August while still on territory, and (3) had high site fidelity across years. Third, we focused only on plumage coloration, and other ornaments (e.g., mask, crown, and beak coloration) of cardinals also may be important indicators of quality (Jawor and Breitwisch 2004). Our study provides some evidence that urban disturbances can influence plumages of Northern Cardinals in our system, but continued study is needed to identify and understand the underlying mechanisms of plumage differences.

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ANNUAL PRECIPITATION AFFECTS REPRODUCTION OF THE SOUTHERN GREY SHRIKE (*LANIUS MERIDIONALIS*)

ODED KEYNAN[1] AND REUVEN YOSEF[2,3]

ABSTRACT.—We studied the breeding ecology of the Southern Grey Shrike *(Lanius meridionalis)* at the Shezaf Nature Reserve, Arava Valley, Israel, an extremely arid desert with mean annual rainfall of 30 mm. We color-banded 128 shrikes during 2007–2009. The breeding season lasted from late February until late June. We found 34 nests and a correlation between years with amount of precipitation and number of breeding pairs. Second broods after successful broods were found only in 2007 and were all unsuccessful. Most nests were in *Acacia* trees; pairs that nested in dry trees, lacking foliage, were more likely to fail. The average clutch size was 3.44; average number of nestlings was 1.95; and average number of nestlings that fledged was 1.24. These results are lower than other studies of the species, probably a result of the scarcity of food in the arid environment. Nest survival rate was higher during incubation than during rearing of nestlings (0.71vs. 0.62), and total nest survival was 44.5%. The arid Arava Valley influences breeding success of Southern Grey Shrikes, and the present severe drought could negatively influence persistence of the shrike population in the Arava Valley. *Received 6 September 2009. Accepted 23 November 2009.*

Rainfall is known to have profound effects on the life history of many bird species and different populations within species (Lloyd 1999, Morrison and Bolger 2002, Mondajem and Bamford 2009). Water is a strong limiting factor in arid ecosystems, where rainfall is generally low, erratic, and unpredictable (Noy-Meir 1973). This leads to low primary productivity and low food availability when combined with high temperatures (Tieleman et al. 2004). Birds that reproduce in arid ecosystems respond to these limiting factors by reducing clutch size (Lloyd 1999, Tieleman et al. 2004) or breeding earlier in the season or by not breeding at all in regions where conditions are particularly unfavorable (Immelmann 1973).

Arid ecosystems are characterized by high between-year variations in both amount and duration of productivity due to the unpredictability of rains (Illera and Diaz 2006). Thus, individual birds that live in these environments must have a high phenotypic flexibility to survive and reproduce (Ricklefs and Wikelski 2002). Lloyd (1999) showed that >50% of the species in South Africa's arid zones had inter-seasonal and inter-annual variations in clutch size due to changes in food availability. Tieleman et al. (2004), in their research on life history variation along an aridity gradient in larks, showed that nest predation increased while both growth rate and clutch size decreased with increasing aridity.

The Southern Grey Shrike (*Lanius meridionalis*) is a passerine (Laniidae). Birds in this family are known for their similarity to diurnal raptors in morphology, especially the strong and sharp bill, and their predatory behavior (Yosef 2008). Shrikes do not posses strong talons, in contrast to raptors, and impaling behavior evolved in the family as a way to dismember prey (Smith 1973).

The Southern Grey Shrike was recently separated from the Great Grey Shrike (*L. excubitor*) (Lefranc and Worfolk 1997). It is widely distributed in the Middle East, North Africa, and central Asia (Lefranc and Worfolk 1997); in Israel, it is resident along the Dead Sea Rift Valley (Shirihai 1996). There are few studies of its reproductive biology in extremely arid ecosystems (e.g., Yosef 1992, Budden and Wright 2000); more research is needed to understand the species' response to extreme aridity and a fluctuating, scarce food base.

Our objectives were to: (1) characterize the breeding ecology of the Southern Grey Shrike in an extremely arid environment, (2) compare it to previous studies on populations of the same species in other and similar environments, and (3) characterize the changes in the reproductive biology within our population following changes in precipitation between years. We hypothesized that, similar to Tieleman et al. (2004), we would find an effect of aridity on reproductive effort and success of the Southern Grey Shrike. We predicted that, because of the reduced prey base in desert areas, the number of clutches of a pair of shrikes in the season would be low due to exposure and lack of appropriate breeding sites.

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METHODS

Study Area.—The study was conducted at the Shezaf Nature Reserve during April 2006 to July 2009 in the southern part of Israel, ~30 km south of the Dead Sea in the Arava Rift Valley between the settlements of Hazeva (30° 46′ N, 35° 16′ E) and Ein Yahav (30° 45′ N, 35° 15′ E). The Arava Valley is an extremely arid zone (UNESCO 1977) with a mean annual winter rainfall of 35 mm that occurs in a range of 6–9 days with large annual variations in total rainfall and temporal and spatial distribution (Anava et al. 2000). The mean temperature during summer is 38° C with daily temperatures that can rise to 49° C (Goldreich and Karni 2001). The flora of the Shezaf Nature Reserve is dominated by Acacia trees (*Acacia tortilis* and *A. raddiana*) and scattered shrubs (*Zilla spinosa*, *Lycium shawii*, *and Haloxylon persicum*) that occur only in the dry river beds (wadis).

Field Procedures.—We color-banded 128 Shrikes for individual recognition. Forty-nine (38.3%) adults were captured in a treadle trap (Yosef and Lohrer 1992) and 79 (61.7%) nestlings were banded at the nest 10–11 days post-hatching. All shrikes were accustomed to presence of human observers. Territories were mapped by watching the shrikes' movements in their home ranges and by watching aggressive behavior towards other shrikes; territory size was calculated as the minimum polygon bounded by defended points of the habitat (Yosef and Grubb 1992).

Nests were located during the breeding season and on each visit were checked to ascertain stage of the reproductive cycle (egg laying, incubation, nestling, fledging). We gathered data for 34 nests (23 in 2007, 11 in 2008) and calculated their probability of survival from incubation to fledging using Mayfield's method (Mayfield 1961, 1975). The average duration of incubation and nestling days were from Yosef (1992). We recorded the height of the nest above ground, the species of tree in which the nest was built, and its condition (dry with no foliage vs. green). Means are expressed (± SD), but groups were compared using Mann Whitney-*U* or χ^2 tests. We chose $P < 0.05$ as the minimum acceptable level of significance.

RESULTS

Breeding Season and Nesting Attempts.—The breeding season lasted from late February until late June with peak breeding activity in March (Fig. 1.). Three pairs had second attempts after successful first broods in 2007. None of these attempts fledged any young. None of the pairs in 2008 had second nesting attempts even after having successfully fledged young from the first brood (Table 1). Three nesting attempts were made following nest failure, and one female nested four times with three different males, but only the fourth attempt was successful (Table 1).

We found 34 nests during the two breeding seasons. There was a significant decline in nesting attempts between 2007 and 2008 (23 vs. 11; $\chi^2 = 4.24$, df = 1, $P = 0.04$; Table 1). We found a significant correlation between number of breeding pairs and amount of precipitation between 2007 and 2009 (Spearman correlation $r_s = 1.00$, $P < 0.0001$, Fig. 2).

Nest Construction.—Thirty-three (97%) nests were in Acacia trees (*Acacia raddiana and A. tortilis*) and one (2.9%) was in a *Commicarpus plumbaginens* bush. Twenty-six (76.5%) nests were in green trees and eight (23.5%) in dry trees ($\chi^2 = 9.529$, df = 1, $P = 0.002$, $n = 34$). Nests in dry trees may have been more likely to fail than those in trees with green foliage (Mann Whitney-*U* $z = -1.445$, $P = 0.09$, $n = 34$). Average nest height was 1.86 ± 0.64 m (range 0.47–3.37). Nest height did not affect breeding success (Spearman correlation $P = 0.49$, $n = 34$ for clutch size, 0.43 for hatching success, 0.47 for fledging success)

Clutch Size and Incubation.—The average clutch size was 3.44 ± 0.89 eggs per nest (2–5) for the two breeding seasons and did not differ between years (Mann Whitney-*U* $z = -0.59$, $P = 0.59$, $n = 28$; Table 1). Only females brooded clutches while males foraged and brought food to the female at or near the nest. Males also guarded the area surrounding the nest tree.

Hatching Success and Nestlings.—The average number of eggs that hatched per nest was 2.14 ± 1.28 (0–4) for all nests and did not differ significantly between years. Nestling success per nest, for pairs that fledged at least one young per nesting attempt, was 2.6 ± 1.03 for the two breeding seasons and did not differ between years (Mann Whitney-*U* $z = -1.2$, $P = 0.23$, $n = 29$) (Table 1). At least one nestling fledged from 20 (58.8%) nests during the entire study. The average number of fledglings per nest was 1.53 ± 1.48 (0–4) and did not differ between years (Mann Whitney-*U* $z = -0.16$, $P = 0.89$, $n = 17$ nests).

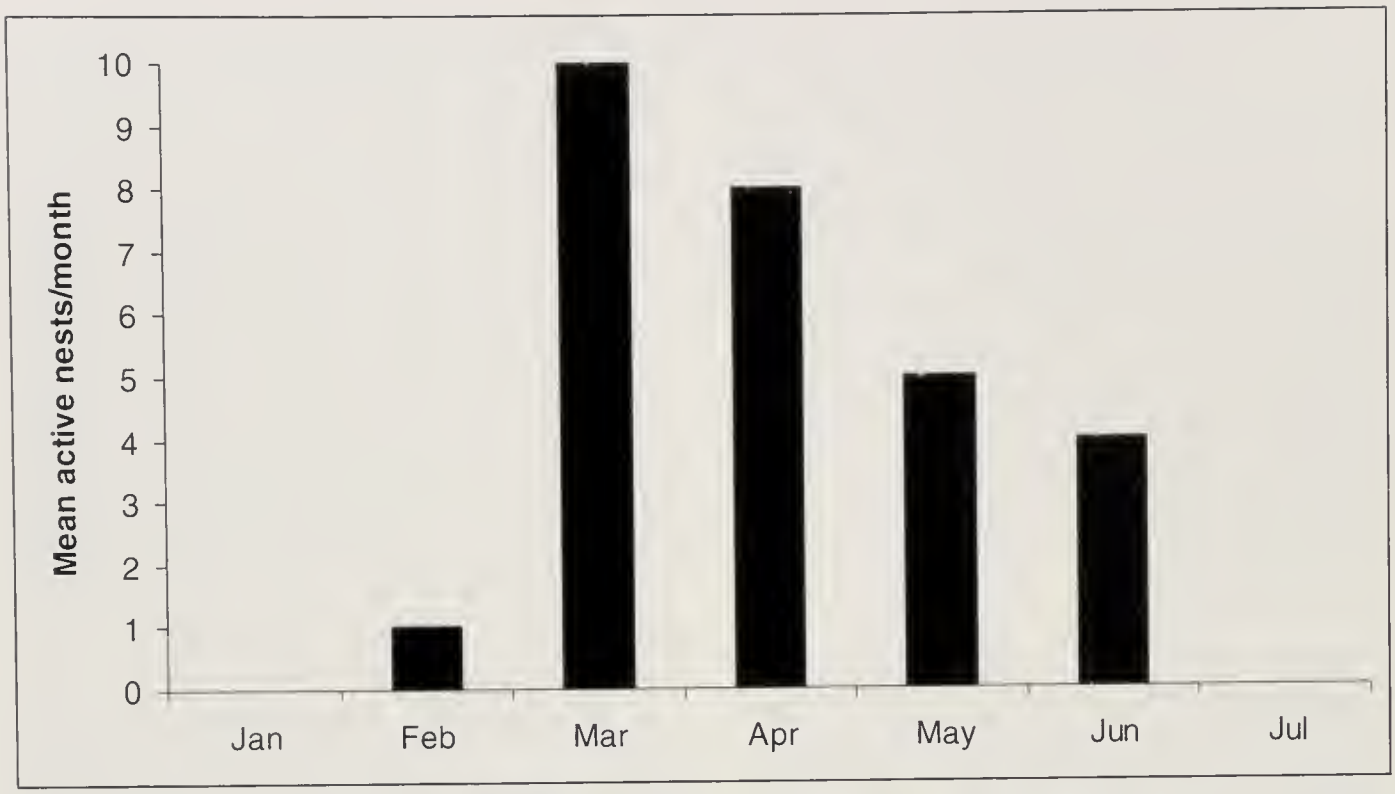

FIG. 1. Average reproductive activity (nests/month) of Southern Grey Shrikes for 2007–2009 in the Shezaf Nature Reserve, Arava Valley, Israel.

Fledglings.—Young remained in the nest tree for 2–5 days post-fledging and both parents cared for them. The young remained with the parents for up to 6 weeks after fledging. Only five (6.3%) of 79 banded nestlings remained in the study area after leaving their parents, and only one (1.3%) fledgling from 2007 bred in the study area in 2008. Both parents cared for the fledglings in the first 3 days after they started to follow the parents in the territory but subsequently the parents separated. In three cases (17.6%), females stopped caring for fledglings and started incubating a second clutch. In six other cases (35.4%), females left the breeding area and left the males to care for the fledglings. In five cases (29.4%) both male and female cared for the fledglings for the entire post-fledging period and, in three cases (17.6%), all fledglings were lost after a few days and the parents separated.

Nest Survival Rate.—Six of 34 nests watched during the incubation period failed while being exposed for 298.5 days for a daily mortality rate of 2% per nest day. Daily nest survival rate was 98%. The survival rate for the entire period was 71%. Seventy-three (74.5%) of 98 eggs laid in 28 nests that succeeded in hatching at least one egg, hatched. Eleven (39.2%) of 28 nests watched during the nestling period failed while being exposed for 408.5 days for a daily mortality rate of 2.3% per nest day. Daily nest survival rate was 97.3%. The survival rate for the entire period was 62.5%. Probability of survival of a nest from start of incubation until the young fledged was $0.71 \times 0.745 \times 0.625 = 0.329$ (i.e., the probability that

TABLE 1. Between season variances ($\bar{x} \pm$ SD) in the nesting ecology of the Southern Grey Shrike in Shezaf Nature Reserve, Israel.

Breeding parameter	2007	2008	Statistics
Breeding pairs	16	9	χ^2 $n = 34$, $\chi^2 = 1.96$, df = 1, $P = 0.16$
Second brood due to failure	4	2	Insufficient data
Second brood after success	3	0	Insufficient data
Breeding attempts	23	11	χ^2 $n = 34$, $\chi^2 = 4.24$, df = 1, $P = 0.04$
Average clutch size	3.52 ± 0.89	3.27 ± 0.90	Mann Whitney-*U* $n = 28$, $z = -0.59$, $P = 0.59$
Average nestlings per nest	2.50 ± 0.78	2.8 ± 1.03	Mann Whitney-*U* $n = 29$ $z = -1.2$, $P = 0.23$
Fledging success	1.17 ± 1.30	1.36 ± 1.39	Mann Whitney-*U* $n = 17$, $z = -0.16$, $P = 0.89$

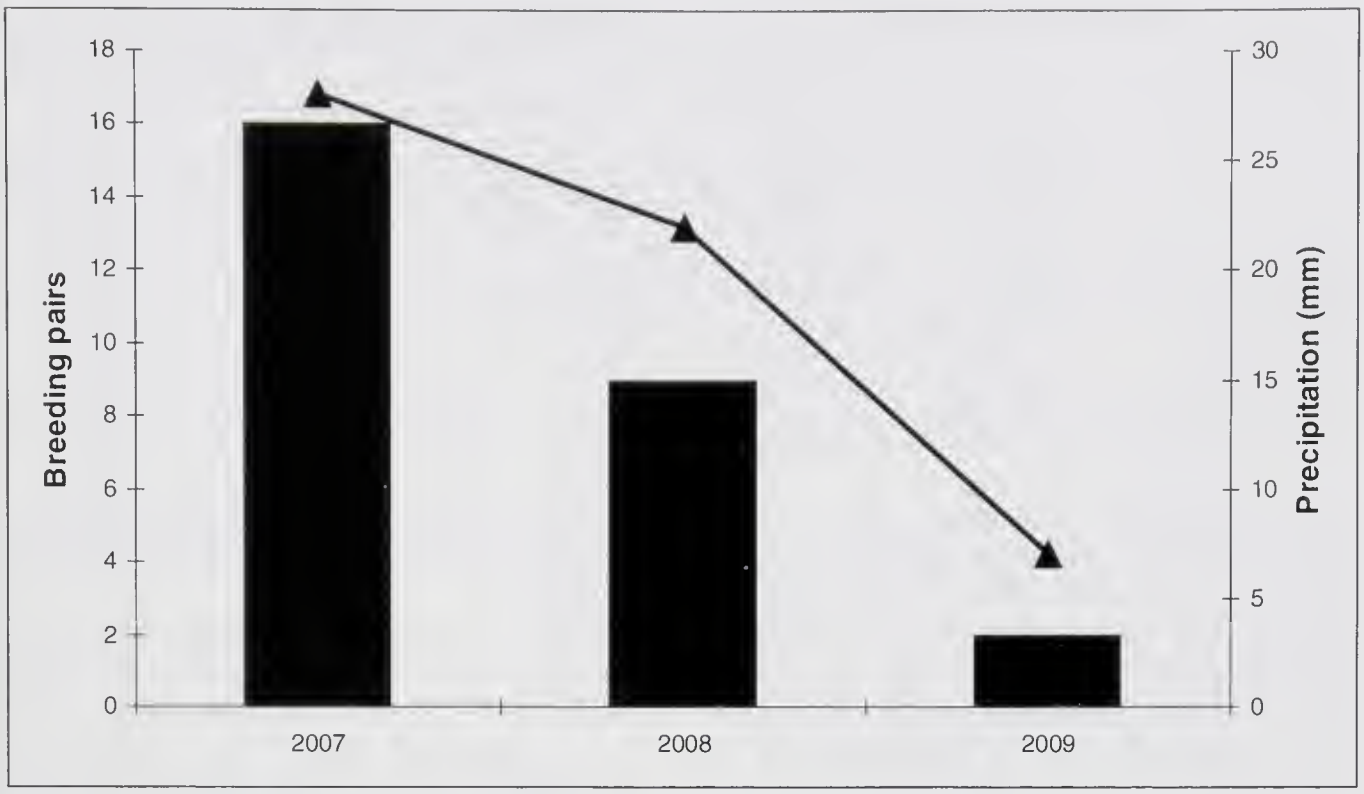

FIG. 2. Number of breeding pairs of Southern Grey Shrikes in Shezaf Nature Reserve, Arava Valley, Israel as a function of annual precipitation (line) between 2007 and 2009.

any nest would fledge at least one young was 32.9%).

DISCUSSION

Our study evaluated the hypothesis that we would find an effect of aridity on reproductive effort and success of the Southern Grey Shrike. Our results are consistent with our predictions that, because of the reduced prey base in deserts, the number of clutches laid by a pair in the season would be low because of exposure and lack of appropriate breeding sites. However, a longer and more detailed study is required to understand the ecological constraints that influence Southern Grey Shrike breeding capability in the desert and their ability to persist in this harsh environment.

The results of the 2007, 2008, and 2009 breeding seasons reflect the combined impact of arid habitats and multi-year drought on the breeding biology of the Southern Grey Shrike at the Shezaf Nature Reserve. Nest survival rate was higher in our study during the incubation period than during the nestling period. This supports our initial prediction that harsh conditions in the Arava affect the breeding success of shrikes. Differences between the incubation and brooding periods can be explained by the need for more food during rearing of the nestlings, a need that was harder to achieve the closer the season was to the summer when prey availability decreases greatly in the desert.

We found no between-year variations in start or length of the breeding season. These findings suggest that, unlike many other avian species, Southern Grey Shrikes do not rely on rain as a stimulus for the onset or end of the breeding season. Differences among regional studies in length of the breeding period (Table 2) also cannot be explained by rainfall. This conclusion does not agree with Illera and Diaz (2006) and Mondajem and Bamford (2009), who suggested that rainfall was the cue that stimulated reproductive activities in birds living in unpredictable environments. Lloyd (1999), however, found rain as a stimulus for breeding activity for only some of the birds of the South African arid zones. We believe Southern Grey Shrikes do not use rainfall as a stimulus for timing and duration of the breeding season because of the wide range of habitats they occupy. Southern Grey Shrikes occur in many habitats that differ in their predictability. Thus, rainfall cannot be a reliable cue for the onset of the breeding season.

The main between-year differences in our study were the number of breeding pairs at the study site and their breeding attempts. Some of the pairs in 2007 attempted second broods after success but

TABLE 2. Life history variances ($\bar{x} \pm$ SD) in the current study in comparison to other reproductive studies of Southern Grey Shrike.

	Current study	Budden and Wright 2000	Inbar 1995	Yosef 1992	Campos et al. 2000	Lepley et al. 2000
Location	Hazeva, Israel	Hazeva, Israel	Mt. Hermon, Israel	Negev Desert, Israel	Northern Spain	Caru-Seche, France
Avg. rainfall (mm)	30	30	1,500	90	325	>500
Breeding season	Feb–Jun	Feb–Jun	Unavailable	Jan–Aug	Mar–Jul	Mar–Jun
Max. # of broods	2	2	Unavailable	4	1	1
Avg. clutch size	3.44 ± 0.89	3.9 ± 0.57	4.6 ± 0.5	5.8 ± 0.6	5.7 ± 0.4	5.2 ± 1.1
Avg. hatchlings/nest	2.14 ± 1.28	1.09	Unavailable	4.7 ± 2.1	2.1 ± 2.4	3.1
Avg. fledglings/nest	1.53 ± 1.48	Unavailable	Unavailable	3.6 ± 1.4	Unavailable	1.54 ± 1.9

all attempts failed. In contrast, none of the pairs in 2008 and 2009 had any signs of trying a second brood. This difference indicates that number of breeding attempts was most probably related to food abundance. Bird species that fledge more than one brood decrease in breeding success as the breeding season advances (Verhulst and Nilsson 2008). This decrease in breeding success occurs mainly because of climatic factors that affect food availability (Takagi 2001, Verhulst and Nilsson 2008, Yosef and Zduniak 2008, Mondajem and Bamford 2009). It is possible that food was so scarce during 2008 that the pairs could invest in only one brood. Southern Grey Shrikes can fledge up to four broods in less arid environments, where food is more abundant and the duration of the breeding season is longer (Table 2).

Far fewer pairs live and breed in the Arava Valley than in the Sede Boker area (Shirihai 1996). We suggest that conditions in the Arava are marginal for the Southern Grey Shrike and are possibly a limiting factor to its distribution. The severe droughts in the past few years have affected the numbers of breeding pairs in the Arava (Fig. 2). The number of pairs declined sharply between years (Table 1), reaching a low of three in 2009 (Fig. 2), and it appears shrikes assess habitat quality before they initiate breeding (Yosef 2008). It is possible that some relocate to other breeding habitats if food availability is low. It is also possible that some individuals that nested during 2007 did not survive the harsh summer or were unable to continue to defend a good territory due to drought.

George et al. (1992) reported that drought severely affected total bird density and breeding success. They showed that some species recovered numbers in the year after the drought but others did not. Bolger et al. (2005) found that an extreme drought dramatically reduced both the number of pairs breeding and breeding success in four species of passerine birds in southern California.

The Southern Grey Shrike population in Shezaf Nature Reserve has declined drastically in the past 3 years, due to a severe drought. It will be of interest to ascertain whether the population can persist and will recover in the future if there are good rains.

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HOME RANGE SIZES AND HABITAT USE OF NELSON'S AND SALTMARSH SPARROWS

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ABSTRACT.—Nelson's (*Ammodramus nelsoni*) and Saltmarsh (*A. caudacutus*) sparrows are sympatric breeders in tidal marshes of the southern Gulf of Maine. These sparrows hybridize, have different mating strategies, and males do not defend territories or provide parental care. We estimated and compared core area sizes, home range sizes, and habitat use between species and between males and females. We radio-marked 140 sparrows (63 Nelson's and 77 Saltmarsh sparrows) during three breeding seasons (1999–2001) at Scarborough Marsh, Maine, USA. Home ranges of male *A. nelsoni* were 2.3 times larger (± SE) (119.68 ± 19.43 ha) than those of male *A. caudacutus* (52.85 ± 8.68 ha). Home range sizes of female Nelson's and female Saltmarsh sparrows did not differ from each other (female Nelson's home range = 43.58 ± 13.10 ha; female Saltmarsh home range = 27.81 ± 6.3 ha). More than 40% of male and 18% of female home ranges had two discrete core areas and, in most instances, each core area corresponded to a separate lunar cycle. We suggest that differences in mating strategies, densities, and adaptation to nesting in tidal marshes explain the larger home range estimates for male Nelson's Sparrows. Female and male Nelson's Sparrows' home ranges had more *Spartina alterniflora* cover and female Saltmarsh Sparrows' home ranges had greater *Juncus gerardii* cover than random locations. Home ranges of female Saltmarsh Sparrows had less *Spartina alterniflora* cover and more *Juncus gerardii* cover than female Nelson's Sparrows. We did not detect any differences in vegetation variables between male Saltmarsh and male Nelson's sparrow home ranges.
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Home range and resource use can occur at multiple spatial and temporal scales that may change during the annual cycle for most bird species. Movement patterns and space requirements are important parameters to consider when attempting to understand populations and how they might respond to different management actions or habitat change scenarios (Barbour and Litvaitis 1993). Home range studies can provide valuable information about habitat selection, use of space, and in making predictions about how environmental change can alter a species' available habitat (White and Garrott 1990).

Nelson's (*Ammodramus nelsoni* previously known as Nelson's Sharp-tailed Sparrow [AOU 1998, Chesser et al. 2009]) and Saltmarsh (*A. caudacutus* previously known as Saltmarsh Sharp-tailed Sparrow [AOU 1998, Chesser et al. 2009]) sparrows are listed as conservation priorities due to our limited understanding of their basic demographic parameters and habitat requirements (Rich et al. 2004). Previous research into the breeding ecology of these sparrows has described responses to landscape features (Benoit and Askins 1999, Shriver et al. 2004), dispersal patterns and survival rates (DiQuinzio et al. 2001), and second (Nocera et al. 2007) and third (Woolfenden 1956, Greenlaw and Rising 1994) order habitat selection (Johnson 1980). These studies have increased our understanding of the breeding ecology for these taxa from Long Island, New York, USA (Woolfenden 1956, Greenlaw and Rising 1994) to the Canadian Maritimes (Nocera et al. 2007), supporting the species split (AOU 1995). These aid in making predictions about how changes to available habitat may affect the persistence of populations of these species. Our objectives were to: (1) use radiotelemetry to estimate species- and male/female-specific home range size, and (2) resource use to further our understanding of how these non-territorial and promiscuous (Greenlaw and Rising 1994) species use their breeding habitat.

METHODS

We used mist nests to capture sparrows at Scarborough Marsh, Maine, USA (43° 34′ N, 70° 22′ W) during three breeding seasons (20 May–15 Aug) from 1999 to 2001. All sparrows were individually marked with a U.S. Geological Survey band and 3 color bands. We conducted

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our study on a 100-ha portion of this 1,500-ha salt marsh. *Spartina patens*, *S. alterniflora*, *Distichlis spicata*, *Juncus gerardii*, and salt pans (depressions with little or no vegetation and generally high salinity levels) dominated this area of Scarborough Marsh.

We used radiotelemetry to relocate individuals in the marsh by homing during each of three breeding seasons. We attached 1-g radio transmitters (<5% body mass, Holohil Systems Ltd., Carp, ON, Canada) to adult males and females of both species using the thigh-harness method (Rappole and Tipton 1991). We assessed the fit of transmitters using a 30 × 25 × 25 cm, slotted, clear-plastic cage to view sparrows after transmitter attachment; if a harness and transmitter did not appear to fit properly, we removed it and released the sparrow. We attempted to locate radio-marked birds each day by homing using a receiver (Communication Specialists Inc., Orange, CA, USA) and 4-element, hand-held antenna. We recaptured as many birds as possible at the end of the season to remove transmitters.

The surface complexity and zonation of the marsh vegetation in our study area facilitated accurate plotting of sparrow locations. We used a high resolution, color–infrared, aerial photograph to record locations of individual sparrows each field day until batteries in transmitters failed or transmitters were removed. This geo-referenced photograph allowed us to plot locations of sparrows to within 3 m. We overlaid a transparency on the photograph each field day, and marked date, sparrow locations, transmitter frequency, band number, species, and male or female on the overlay. We examined the dominant vegetation within a 1-m-radius circle of each sparrow location and categorized vegetation as: (1) *Spartina alterniflora*, (2) *S. patens*, (3) *S. patens*/*S. alterniflora*, (4) *Juncus gerardii*, (5) *Distichlis spicata*/*S. patens*, (6) un-vegetated salt pan, or (7) vegetated salt pan. We used the proportion of each vegetation type across all locations for a specific sparrow in the habitat use analysis. We also sampled 174 randomly located 1-m-radius circular plots to estimate the availability of each vegetation type within the study area. We used the geo-referenced photograph as the base layer to digitize these data using ArcView 3.3 and used the animal movement extension (Hooge and Eichenlaub 1997) to estimate 50% (hereafter, core area) and 95% (hereafter, home range) fixed kernel home ranges. We used only those individuals with ≥20 locations for all analyses. We used univariate ANOVA to test for differences in core area and home range sizes between species and males/females (Zar 1999). We calculated the number of sparrows that had two discrete core areas (i.e., two 50% kernel home ranges) and measured the distance between the centroids for each core area. We used univariate ANOVA with Tukey HSD *post-hoc* tests to explore differences in vegetative cover between randomly located points, and locations of males and females for each species, and between the two species. We used a Kolmogorov-Smirnov goodness of fit test to examine if each variable fit a normal distribution (Zar 1999). All statistical tests were conducted in SPSS (Version 16.0) with $alpha = 0.05$.

RESULTS

We estimated core area and home range size for 63 radio-marked Nelson's and 77 radio-marked Saltmarsh sparrows at Scarborough Marsh, Maine in 1999–2001. Core area and home range sizes of males were larger than for females, both for Nelson's (core area: $F_{1,62} = 8.5$, $P = 0.005$; home range: $F_{1,62} = 11.1$, $P = 0.001$) and Saltmarsh sparrows (core area: $F_{1,76} = 4.2$, $P = 0.045$; home range: $F_{1,76} = 5.7$, $P = 0.019$) (Table 1). Both core area and home range sizes of male Nelson's Sparrows were larger than those of male Saltmarsh Sparrows (core area: $F_{1,61} = 4.3$, $P = 0.043$; home range: $F_{1,61} = 10.6$, $P = 0.002$) (Table 1). We found no difference in core area or home range sizes of female Nelson's and female Saltmarsh sparrows (core area: $F_{1,77} = 0.18$, $P = 0.674$; home range: $F_{1,77} = 1.1$, $P = 0.289$) (Table 1). Distances between core areas, for those individuals that maintained two core areas, were greater for male Nelson's than for male Saltmarsh sparrows ($F_{1,54} = 4.5$, $P = 0.038$), and were greater for female Nelson's compared to female Saltmarsh sparrows ($F_{1,34} = 8.0$, $P = 0.008$) (Table 1).

Female and male Nelson's Sparrows' home ranges had more *Spartina alterniflora* cover than random locations ($F_{1,237} = 16.2$, $P < 0.001$) but did not differ between each other ($P = 0.142$). The amount of *S. patens* cover differed among Nelson's Sparrows and random locations ($F_{1,237} = 6.7$, $P = 0.002$) with less *S. patens* in the home ranges of male Nelson's Sparrows ($P < 0.001$, Table 2). *Spartina patens*/*S. alterniflora* cover differed among Nelson's Sparrows and random

TABLE 1. Characteristics ($\bar{x}$ ± SE) of radio-marked Nelson's and Saltmarsh sparrows fixed kernel 50% core areas and 95% home ranges at Scarborough Marsh, Maine, USA, 1999 to 2001.

Variable	Nelson's Sparrow		Saltmarsh Sparrow	
	Females (n = 34)	Males (n = 29)	Females (n = 44)	Males (n = 33)
Core area, ha	6.15 ± 1.66	18.42 ± 3.91	5.25 ± 1.38	9.64 ± 1.67
Home range, ha	43.58 ± 13.10	119.68 ± 19.4	27.81 ± 6.30	52.85 ± 8.68
Home ranges with two cores	9 (27%)	13 (45%)	8 (18%)	14 (42%)
Core area distance, m	161.40 ± 38.85	204.28 ± 25.61	77.56 ±13.16	158.99 ± 17.55

locations ($F_{1,237}$ = 5.2, P = 0.006) with less *Spartina patens*/*S. alterniflora* in male Nelson's Sparrow home ranges (P = 0.018, Table 2). Both male and female Nelson's Sparrow home ranges had more vegetated pan cover than random locations ($F_{1,237}$ = 38.1, P < 0.001, Table 2).

Spartina alterniflora cover differed among Saltmarsh Sparrow home ranges and random locations ($F_{1,252}$ = 8.4, P < 0.001, Table 2) with greater cover in male Saltmarsh Sparrow home ranges than in random locations (P < 0.001). *Spartina patens* cover differed among Saltmarsh Sparrow home ranges and random locations ($F_{1,252}$ = 6.6, P = 0.002, Table 2) with less cover in home ranges of male Saltmarsh Sparrows than in random locations (P = 0.004). *Spartina patens*/*S. alterniflora* cover differed among Saltmarsh Sparrow home ranges and random locations ($F_{1,252}$ = 5.5, P = 0.005, Table 2) with less cover in home ranges of male (P = 0.039) and female (P = 0.004) Saltmarsh Sparrows than in random locations (Table 2). *Juncus gerardii* cover differed among Saltmarsh Sparrow home ranges and random locations ($F_{1,252}$ = 7.1, P = 0.001, Table 2) with more cover in female Saltmarsh Sparrow home ranges than in random locations (P = 0.001, Table 2). Both male and female Saltmarsh Sparrow home ranges had more vegetated pan cover than random locations ($F_{1,237}$ = 48.2, P < 0.001, Table 2). Female Saltmarsh Sparrow home ranges had more *Spartina alterniflora* cover ($F_{1,79}$ = 4.5, P = 0.038) and more *Juncus gerardii* cover ($F_{1,79}$ = 4.6, P = 0.035) than female Nelson's Sparrow home ranges (Table 2). We did not detect any differences in vegetation variables between home ranges of male Saltmarsh and male Nelson's sparrows (Table 2).

DISCUSSION

Home range sizes of both species were 2–10 times larger than those reported for other emberizid sparrows (Patterson and Petrinovich 1978, Reed 1985, Delany et al. 1995, Bechtoldt and Stouffer 2005, Jones and Bock 2005, Cox and Jones 2007). Male/female-specific home range size was approximately twice as large for Nelson's than for Saltmarsh sparrows. Male Nelson's Sparrow home range sizes were three times larger than those of females. All home ranges for both species and males and females overlapped within the 100-ha study area. Home range sizes for male Saltmarsh Sparrows were twice those of females, but both were smaller than home ranges of male Nelson's Sparrows. Woolfenden (1956) estimated male Saltmarsh Sparrow home ranges to be 3–4 times larger (1.2–1.6 ha for

TABLE 2. Proportion ± SE of seven vegetation types within Nelson's and Saltmarsh sparrow home ranges and at random points at Scarborough Marsh, Maine, 1999–2001.

Vegetation type	Nelson's Sparrow		Saltmarsh Sparrow		
	Females	Males	Females	Males	Random
Spartina alterniflora	0.188 ± 0.021	0.288 ± 0.041	0.132 ± 0.017	0.216 ± 0.032	0.069 ± 0.017
S. patens	0.276 ± 0.023	0.178 ± 0.021	0.288 ± 0.029	0.201 ± 0.025	0.435 ± 0.031
S. patens/*S. alterniflora*	0.104 ± 0.021	0.044 ± 0.010	0.087 ± 0.013	0.081 ± 0.029	0.239 ± 0.030
Juncus gerardii	0.186 ± 0.025	0.214 ± 0.030	0.283 ± 0.035	0.216 ± 0.042	0.115 ± 0.022
Distichlis spicata	0.012 ± 0.007	0.006 ± 0.005	0.006 ± 0.003	0.001 ± 0.001	0.008 ± 0.006
Un-vegetated Pan	0.005 ± 0.002	0.013 ± 0.005	0.004 ± 0.001	0.015 ± 0.006	0.041 ± 0.014
Vegetated Pan	0.188 ± 0.021	0.203 ± 0.032	0.155 ± 0.021	0.235 ± 0.030	0.019 ± 0.009

males vs. 0.4 ha for females) than those of females. Greenlaw and Rising (1994) also reported a 4-fold difference in male (4.3 ha) versus female (1.1 ha) home range size from studies of Saltmarsh Sparrows. It is difficult to compare our findings with other home range estimates given our use of radiotelemetry. The non-territorial mating system of these sparrows (Woolfenden 1956, Murray 1969, Post and Greenlaw 1982, Greenlaw 1993, Shriver et al. 2007) generally results in more time spent by males searching for receptive females or females soliciting copulatory chases (Greenlaw and Rising 1994, Shriver et al. 2007). This, coupled with a lack of territorial boundaries, partially explains the large home ranges observed for both taxa in our study.

Male Nelson's Sparrows had 33% larger home ranges than male Saltmarsh Sparrows which may be explained by differences in mating systems and breeding densities between the two species. Male Nelson's Sparrows spend a substantial amount of time guarding females (up to 43 hrs with the same female, Shriver et al. 2007) while male Saltmarsh Sparrows practice "scramble competition polygyny" (Greenlaw and Rising 1994) where small groups (3–6) of males chase receptive females, copulate, and then usually perch to search for another receptive female (W. G. Shriver et al., unpubl. data). Male Saltmarsh Sparrows have not been observed guarding females (Shriver et al. 2007). Twenty-seven percent of female Nelson's Sparrows maintained two distinct core areas and the distance between these core areas was two times greater than for female Saltmarsh Sparrows. This may cause male Nelson's Sparrows to travel farther to encounter females compared to male Saltmarsh Sparrows. We estimated there were three times more female Saltmarsh Sparrows than female Nelson's Sparrows (1998 to 2001; W. G. Shriver et al., unpubl. data) in our study area. We suggest, based on our banding data from this site, greater dispersion of female Nelson's Sparrows (especially in lower density areas), greater distances between female Nelson's Sparrows' core areas, and the mate guarding behavior of male Nelson's Sparrows, at least partially explain differences in home range sizes for these species.

Other aspects of sharp-tailed sparrow breeding ecology appear to be synchronous with new moon tidal events (Shriver et al. 2007) and we reviewed the timing of the maintenance of each core area. More than half of the sparrows with two discrete core areas did not use them simultaneously, but instead core area use was timed with separate lunar cycles. Most nests typically flood during spring tides (Gjerdrum et al. 2005, Shriver et al. 2007), and it is apparent that re-nesting female sparrows moved within the study area to construct a second nest (during the subsequent lunar event). The large ranges (and multiple core areas) of males are likely a consequence of spatial shifts exhibited by females. Female Nelson's Sparrows do not re-nest immediately after a flooding event (Shriver et al. 2007), and appear to move further to re-nest than female Saltmarsh Sparrows. Home ranges of male Nelson's Sparrows, therefore, are larger and distance between cores further as they attempt to maintain close proximity to females during re-nesting attempts.

Patterns in habitat use for these sparrows differed from studies of nest site selection (DiQuinzio et al. 2002, Gjerdrum et al. 2005, Shriver et al. 2007). We found sparrows more frequently in *Spartina alterniflora* and *Juncus gerardii* cover and less often in *S. patens* cover than was available in the study area. Vegetated pan cover was also more common within sparrow home ranges than was available in the study area. Saltmarsh Sparrow female home ranges had the greatest proportion of *Juncus gerardii* compared to random locations or other sparrow home ranges. Gjerdrum et al. (2008) also found *Juncus gerardii* was the key predictor variable in explaining variation in number of nests and fledgling production.

Tidal marshes are limited globally in extent to 45,000 km^2 with 15,500 km^2 (34%) occurring along the Atlantic and Gulf coasts of North America (Bertness 1999, Mendelssohn and Mckee 2000, Greenberg et al. 2006). The coastlines of North America support the greatest number of endemic tidal marsh vertebrate species, including Saltmarsh Sparrows (Greenberg et al. 2006), increasing the global significance of these ecosystems. Resource professionals engaged in tidal marsh conservation have reason to be concerned about persistence of tidal marsh vertebrate species given their geographically limited habitat and vulnerability to habitat loss and fragmentation resulting from sea level rise. Even moderate estimates (30 cm rise) of sea level rise had negative effects on the estimated persistence of Seaside Sparrows (*Ammodramus maritimus*) in Connecticut (Shriver and Gibbs 2004). Our study was conducted in one of the larger marshes in the Gulf of Maine where these species co-occur, near

the northern limit of Saltmarsh Sparrows and the southern limit of Nelson's Sparrows. These conditions certainly influence the spatial use patterns of these sparrows and our estimates of home range size for these taxa may not apply to smaller sites where these sparrows are relatively common and allopatric. Future home range studies at other sites using similar techniques would be valuable to examine the variation in these parameters given different marsh sizes and location within the range of each species. Space requirements and habitat use information similar to those presented here and elsewhere (Gjerdrum et al. 2008) could then be used to model the effects of climate change on these species which would aid in conservation planning efforts.

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ASSESSING GENERALIZED EGG MIMICRY: A QUANTITATIVE COMPARISON OF EGGS OF BROWN-HEADED COWBIRDS AND GRASSLAND PASSERINES

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ABSTRACT.—Perceived similarity in appearance of eggs of the Brown-headed Cowbird (*Molothrus ater*) and several grassland passerine hosts has been suggested to represent a form of generalized mimicry evolved to impede egg discrimination. We tested this hypothesis by quantitatively comparing four parameters (ground color, maculation color, distribution of maculation, and maculation density) among cowbird eggs and those of six grassland passerines known to preferentially accept cowbird eggs over non-mimetic blue eggs. Cowbird eggs did not significantly differ in three of four parameters (mean ground color, and color and density of maculation) from the average grassland passerine egg measured for this community, in southern Saskatchewan, when all grassland passerine eggs were pooled. Cowbird eggs sufficiently overlapped grassland passerine eggs in these three parameters that 88% of cowbird eggs measured were statistically indistinguishable from among all grassland passerine eggs. The frequency at which cowbird eggs were misclassified as eggs of each grassland passerine ranged from 8 to 48%, which suggests that a single cowbird egg is capable of mimicking the eggs of more than one species. These results support the hypothesis that cowbirds have evolved a generalized egg appearance that mimics the eggs of multiple grassland passerine hosts within a single community. *Received 31 October 2008. Accepted 23 October 2009.*

Evolution of egg mimicry by obligate brood parasites is regarded as one of the most common responses to development of egg discrimination and ejection by intolerant hosts (Underwood and Sealy 2002, Kilner 2006). Egg mimicry evolves because ejection of unlike eggs by hosts provides a selective advantage to parasitic eggs that match the clutch in which they are laid (Davies and Brooke 1991, Soler et al. 2003). The extent of similarity gradually escalates through a co-evolutionary race as hosts refine their egg-discrimination abilities over subsequent generations (Moksnes et al. 1990, Davies and Brooke 1991). The evolutionary equilibrium hypothesis posits that whenever the level of mimicry exceeds a species' ability to discriminate between eggs, the host accepts the parasitic egg (Davies and Brooke 1988, Lotem and Nakamura 1998). Presumably, acceptance occurs because of the greater cost of mistakenly ejecting the wrong egg (Davies and Brooke 1988, Lotem and Nakamura 1998).

Egg mimicry has been documented or suspected in several parasitic systems (Underwood and Sealy 2002). Most notably different groups of female Common Cuckoos (*Cuculus canorus*) have evolved eggs that closely mimic those of a preferred host (Davies and Brooke 1988, Marchetti et al. 1998, Gibbs et al. 2000). The Brown-headed Cowbird (*Molothrus ater*, hereafter cowbird) has been largely exempt from these speculations (Sealy et al. 2002, Mermoz and Ornelas 2004) because individual female cowbirds are known to parasitize multiple species (Fleischer 1985, Alderson et al. 1999). Rothstein (2001) suggested cowbird egg mimicry could not evolve due to the immense variability in egg appearance each female cowbird would encounter when parasitizing several species. He also argued that because cowbirds are known to parasitize hundreds of species it would be more beneficial to avoid hosts that discriminate among eggs than to enter a costly co-evolutionary race. A recent comparison of tolerant and intolerant hosts of the cowbird also found that egg appearance was not correlated with acceptance of cowbird eggs (Peer and Sealy 2004).

The close resemblance in color and maculation pattern between cowbird eggs and those of many grassland passerines, despite skepticism, has been suggested to be a form of generalized egg mimicry (Peer et al. 2000, Davis et al. 2002, Frontispiece in Klippenstine and Sealy 2008). Generalized cowbird egg mimicry is the idea that cowbird eggs have been adapted to match the appearance of eggs laid by multiple hosts. The eggs of a parasite in traditional mimicry evolve to resemble those of a single, intolerant host species (Underwood and Sealy 2002). Generalized egg mimicry, however, incorporates the selective

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forces provided by all hosts exhibiting egg discrimination. This causes the parasite's eggs to assume the average color and maculation pattern of eggs from all intolerant hosts in proportion to the selective pressure provided by each host. A single parasite egg can be laid randomly in any host nest in true generalized egg mimicry and still have a high probability of matching the host's eggs.

Indirect evidence of generalized cowbird egg mimicry has come from experiments that showed several grassland passerines accept cowbird eggs despite possessing an ability to eject less mimetic foreign eggs (Peer et al. 2000, Davis et al. 2002, Klippenstine and Sealy 2008). Therefore, the tolerance of parasitism observed in grassland passerines has, in part, been attributed to their inability to identify cowbird eggs among their clutch, i.e., evolutionary equilibrium hypothesis (Peer et al. 2000, Davis et al. 2002, Klippenstine and Sealy 2008). Generalized cowbird egg mimicry is plausible because most grassland passerine eggs are similar in color and maculation pattern (Peer and Sealy 2004, Klippenstine and Sealy 2008). Grassland passerines also are historic hosts of cowbirds and, presumably, have been exposed to parasitism sufficiently long for the required coevolutionary race to have occurred (Mayfield 1965, Rothstein 1994, Igl and Johnson 2007).

We quantitatively compared color and maculation pattern of cowbird eggs to eggs of a community of grassland passerines known to accept cowbird eggs, but eject non-mimetic eggs, to examine the possibility of generalized cowbird egg mimicry (Klippenstine and Sealy 2008): Sprague's Pipits (*Anthus spragueii*), Vesper Sparrows (*Pooecetes gramineus*), Savannah Sparrows (*Passerculus sandwichensis*), Baird's Sparrows (*Ammodramus bairdii*), Chestnut-collared Longspurs (*Calcarius ornatus*), and Western Meadowlarks (*Sturnella neglecta*). We predicted if generalized cowbird egg mimicry has evolved that: (1) cowbird eggs would match the average color and maculation pattern present among the eggs of all six grassland passerines; (2) cowbirds would have incorporated enough of the community-wide variation that a proportion of their eggs would match those of each grassland passerine; and (3) an individual cowbird egg would be capable of mimicking the eggs of more than one species.

METHODS

Fieldwork was conducted in southcentral Saskatchewan, Canada from 7 May to 1 July 2001 and 9 May to 15 July 2002. Sites were 60 km south of Regina within a 100-km^2 area centered about the abandoned hamlet of Dummer (49° 50′ N, 104° 49′ W). Nests were found in cultivated and uncultivated land using predominantly a dragging rope as described by Klippenstine and Sealy (2008).

Photographs of Eggs.—Appearance of cowbird eggs and grassland passerine eggs was quantified using photographs taken with a 35-mm Pentax automatic focus camera and 100-speed color Kodak film for increased resolution (Fleischer and Smith 1992). Photographs of complete clutches were desired unless this was not possible because of partial predation, cowbird parasitism, or if eggs broke when handled. Cowbird eggs were photographed whenever a nest was naturally parasitized and were included in the photograph of the host's eggs.

All eggs were temporarily placed in an egg box, which measured ~20 by 50 cm and had a foam mat on the bottom with six indentations that held the eggs in place during each photograph. Three color chips (red, green, and blue), each with three shades of their corresponding color (light, medium, and dark), were placed on the mat and included in the photograph (Fleischer and Smith 1992, Villafuerte and Negro 1998). The egg box was placed in a portable hood to exclude outside lighting and a camera stand within the hood was used to ensure consistent photography. Films were developed as 4 × 6 color prints with a matte finish to decrease glare. Photographs in 2001 were developed throughout the field season, but all photographs in 2002 were developed on the same day to reduce variation in color, contrast, and brightness caused by developing at different times. Prints were scanned with a flatbed scanner at 300 dpi for digital analysis.

Measurements of Egg Parameters.—Four egg parameters were measured: ground color, maculation color, distribution of maculation, and total density of maculation. Eggs were isolated from their respective photographs using the magic wand tool of Adobe Photoshop 4.0 to enhance the accuracy of measurements. Maculation was measured using inverted black and white images of each egg. Markings were highlighted as bright white spots, leaving the ground color of the egg black. The proportion of maculation on the blunt and pointed ends of each egg was measured by centering a 20- × 30-pixel rectangular, selection box one-quarter the distance from the pointed end

and one-quarter from the blunt end of each egg, and measuring the proportion of area covered in white compared to black using the Northern Eclipse Program (modified from Fleischer 1985). Density of maculation was calculated as the percent total area covered in maculation for both blunt and pointed ends of each egg on a scale of 0 to 100, i.e., percent ×100. The distribution of maculation was calculated as the percent of the total density of maculation occupying only the blunt end, i.e., blunt end maculation divided by total maculation multiplied by 100. Eggs with evenly distributed maculation had values close to 50 and values increased as the proportion of maculation on the blunt end of the eggs increased.

Ground and maculation colors were measured from the color images of each egg using the RGB program (Villafuerte and Negro 1998). Three samples of ground color were captured using Adobe Photoshop 4.0, i.e., three square 10 × 10 pixels, along the length of the egg, and avoiding the area of brightness caused by glare of the camera's flash. Three to six spots or scrawls were sampled in the case of maculation. All selected areas were transferred into the RGB program, which calculated the red, green, and blue value of each pixel on a scale of 0 to 256 (Villafuerte and Negro 1998). The average red, green, and blue values were assigned to the background color and color of maculation for each species' egg. Preliminary analyses revealed that for eggs of all species the proportion of red, green, and blue was highly correlated to each other in both ground color and maculation color, respectively. The amounts of red, green, and blue for both maculation and ground color were summed because they were not independent; the new value approximated the darkness or lightness of the color on a scale of 0 to 768 with an egg's color becoming darker as this number decreased. This was possible because ground color and maculation color of each species' eggs examined tended to be brown, differing only in intensity of color, which would be seen as lightening or darkening. The correlation between red, green, and blue would have been lower or absent had different colors, i.e., blue, pink, etc., been abundant on the eggs.

The extent to which the shade of each color varied within a photograph due to minor differences in illumination, development, and film was calculated by measuring the discrepancy between observed and theoretical values for the three shades of the color chips photographed with the eggs. A correction factor was computed that represented how much red, green, and blue was added or subtracted from the photograph during its exposure and development (Villafuerte and Negro 1998). This correction factor was calculated for each photograph by averaging the differences between theoretical and observed values for all three shades of each color.

Statistical Analyses.—Eggs of all six grassland passerines were pooled to calculate the average parameters for this community. The total number of eggs for each species was reduced to 15 by randomly eliminating additional eggs to ensure that all species were represented equally when pooled. All reductions were repeated twice and the results were compared to ensure that no bias occurred during the initial reduction. Only 14 Sprague's Pipit eggs were available for comparison, and the average of all 14 eggs was inserted to make up the missing value (Zar 1996). We opted to pool the eggs of each species in equal proportions rather than in proportion to their frequency of parasitism, relative abundance or frequency of cowbird egg ejection, i.e., as a measure of selective pressure, for two reasons: (1) these parameters do not vary significantly among species within this community (Davis 2003, Klippenstine and Sealy 2008); and (2) currently, levels of parasitism and relative abundance of each species varies between years and habitat structure (Davis 2003, Klippenstine and Sealy 2008). A single measure of these parameters may not accurately represent the selective pressure provided by each species currently or throughout their co-evolution with cowbirds.

We used Discriminate Analysis (DA) to examine the extent of discrimination possible between cowbird eggs and the average grassland passerine egg using the categories of maculation (density and distribution of maculation) and color (ground and maculation color). An ANOVA was used to identify which parameter or parameters created the difference if discrimination was observed in any of these categories (Manly 1986). All four parameters were recombined, based on the latter analyses, to acquire the correct collection of parameters that minimized discrimination between cowbird eggs and the average grassland passerine egg. The predicted group membership function following a DA was used to assess overlap between cowbird eggs and grassland passerine eggs using minimum discrim-

TABLE 1. Mean parameter values for the average grassland passerine egg and Brown-headed Cowbird eggs.

Species (*n*)	Density of maculation, %	Distribution of maculation, %	Ground color	Maculation color
Average grassland passerine (90)	23.5 ± 2.0	75.8 ± 2.2*	472.1 ± 9.4	372.0 ± 7.1
Brown-headed Cowbird (50)	28.7 ± 2.2	64.3 ± 1.9	453.6 ± 7.2	362.1 ± 6.4

* Differs ($P = 0.05$) from cowbird eggs.

ination parameters. This function works by attempting to re-assign each egg blindly to its correct species, listing the portion of eggs for each species that was misclassified as being the eggs of all other species (Manly 1986). The portion of misclassification between two species' eggs represented the extent of overlap or "mimicry" between their eggs.

The predicted group membership analysis was conducted on two scales to fully assess mimicry: (1) the frequency of misclassification that occurred when eggs of all six grassland species were compared simultaneously with cowbird eggs; and (2) the frequencies of misclassification that occurred when cowbird eggs were compared separately to eggs of each grassland species. We examined whether the sum of misclassification frequencies between cowbird eggs and eggs of each species was greater than the proportion of cowbird eggs misclassified when compared to all species simultaneously to learn whether individual cowbird eggs mimic those of multiple species. If, however, each cowbird egg only matches the eggs of one species, the sum of misclassification frequencies involving each species should be equal to the proportion misclassified when all eggs were compared together. Differences in the frequency of misclassification between species were assessed using a Chi-square test. There was a tendency for greater discrimination because the same data used in the initial DA were used in the predicted group membership (Manly 1986). This analysis was conservative, as it was more likely to separate species than place them together. Statistical significance was set at *alpha* = 0.05 for all analyses, and all average values are given as mean ± SE.

RESULTS

Cowbird Eggs versus Average Grassland Passerine Egg.—Cowbird eggs were indistinguishable in color (ground and maculation combined) from the average grassland passerine egg for this community (DA, $\chi^2_2 = 1.8$, $P = 0.40$; Table 1, Fig. 1), but were readily discernable in maculation (density and distribution of maculation combined; DA, $\chi^2_2 = 13.5$, $P = 0.001$). Dissimilarities in overall maculation resulted exclusively from cowbird eggs being far more evenly maculated than the average grassland passerine egg ($F_1 = 12.3$, $P = 0.001$), as no difference in the total density of maculation was observed between the two groups ($F_1 = 2.5$, $P = 0.17$, Table 1). Thus, minimum discrimination between cowbird eggs and the average grassland passerine egg was achieved by excluding distribution of maculation as a parameter (DA, $\chi^2_3 = 2.8$, $P = 0.43$ vs. $\chi^2_3 = 13.5$, $P = 0.009$ for all four parameters).

Overlap Between Cowbird Eggs and Grassland Passerine Eggs.—The predicted group membership analysis was significantly more likely to misclassify cowbird eggs on the basis of minimum discrimination parameters, i.e., color and total density of maculation, than eggs of all other grassland passerines ($\chi^2_1 > 4.4$, $P < 0.05$ for all species; Table 2). Overall, 88% of cowbird eggs were misclassified compared to 4 to 70% of grassland passerine eggs (Table 2). Between 4 and 67% of grassland passerine eggs were misclassified as being the eggs of another grassland passerine, an indication of the close resemblance between grassland passerine eggs (Table 2).

Between 8 to 48% of cowbird eggs were misclassified, depending on the species, when cowbird eggs were compared to eggs of each species separately using minimum discrimination parameters (Table 3). The sum of all cowbird egg misclassifications for all six species greatly exceeded the proportion of cowbird eggs misclassified when all eggs were compared simultaneously (186 vs. 88%; Tables 2, 3). The proportion of cowbird eggs misclassified did not differ (28 to 49%; $\chi^2_4 = 6.0$, $P = 0.20$) among eggs of Sprague's Pipit, Vesper, Savannah, and Baird's sparrows, and Chestnut-collared Longspurs (Table 3). A substantially lower proportion of cowbird eggs were misclassified as Western

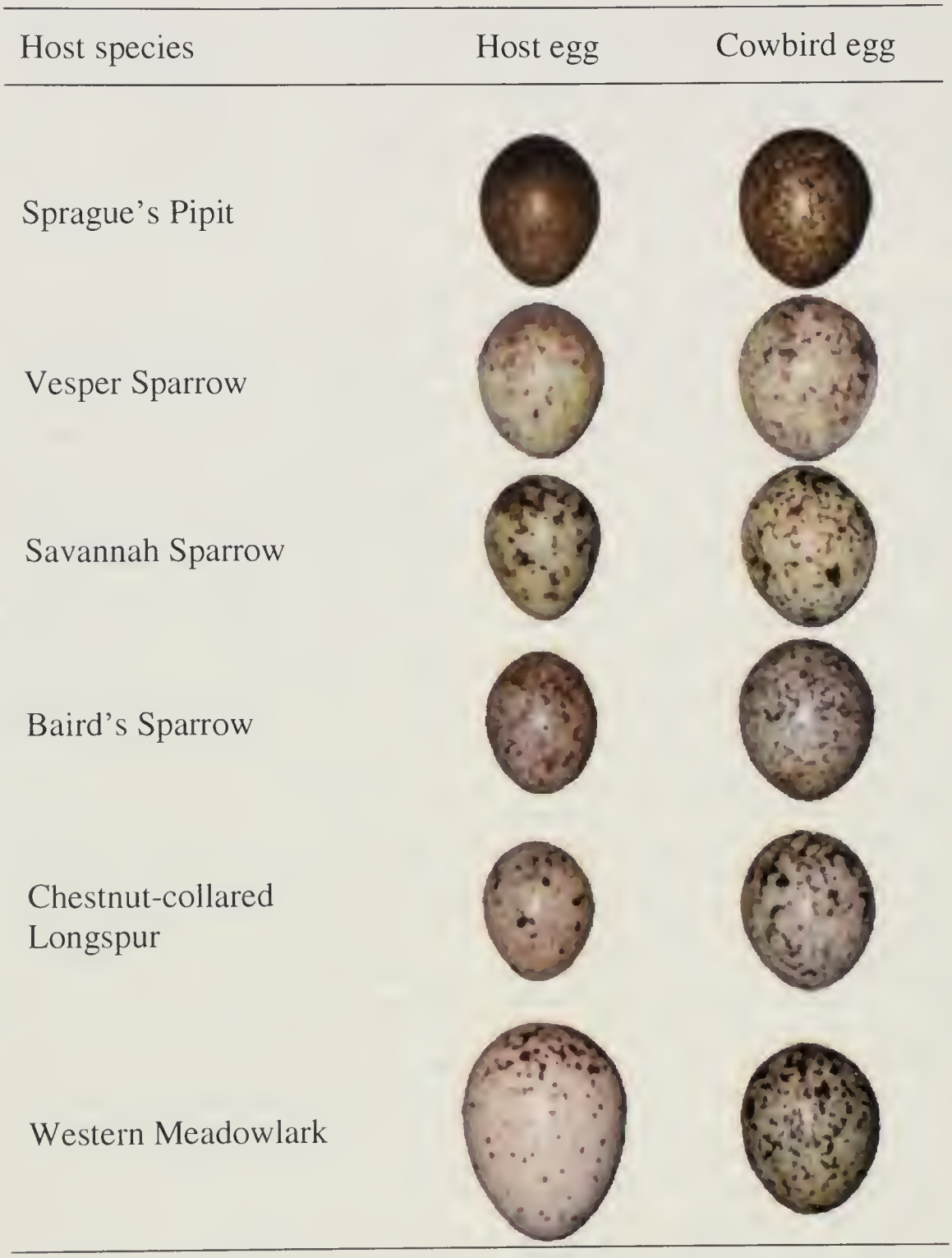

FIG. 1. Examples of remarkable similarities between grassland passerine eggs and cowbird eggs in naturally parasitized nests.

Meadowlark eggs (8%) than the other five species ($\chi^2_1 > 6.7$, $P < 0.05$ for all species; Table 3).

DISCUSSION

Our results support the hypothesis that cowbird eggs have evolved to generally mimic the appearance of eggs from multiple grassland passerines. Cowbird eggs were indistinguishable from the ground and maculation colors, and total density of maculation as measured for the average grassland passerine eggs from this community in southern Saskatchewan (Table 1). All six grassland species examined have been experimentally demonstrated to eject non-mimetic eggs (Klippenstine and Sealy 2008). Thus, our results support the idea that ejection of discordant cowbird eggs has forced them to assume the average appearance of eggs from all intolerant hosts.

Cowbird eggs so closely approximated the color and maculation density of grassland passer-

TABLE 2. Proportion of correct identification and misclassification observed for each species when compared simultaneously using minimum discrimination parameters (ground color, maculation color, and density of maculation).

Species (n)	Eggs correctly identified (%)	Eggs (%) misclassified as... Other grassland passerine eggs	Brown-headed Cowbird eggs	Other species overall
Sprague's Pipit (14)	71	22	7	29
Vesper Sparrow (21)	43	57	0	57
Savannah Sparrow (34)	41	56	3	59
Baird's Sparrow (37)	54	30	16	46
Chestnut-collared Longspur (40)	30	67	3	70
Western Meadowlark (24)	96	4	0	4
Brown-headed Cowbird (50)	12	88		88*

* Differs ($P = 0.05$) from all other grassland passerine eggs.

TABLE 3. Proportion of misclassification observed using minimum discrimination parameters (ground color, maculation color, and density of maculation) between cowbirds eggs and eggs of individual species.

Species (n)	Cowbird eggs misclassified as eggs of each grassland passerine (%)
Sprague's Pipit (14)	28
Vesper Sparrow (21)	38
Savannah Sparrow (34)	36
Baird's Sparrow (37)	28
Chestnut-collared Longspur (40)	48
Western Meadowlark (24)	8*
Total	186

* Differs ($P = 0.05$) from all other grassland eggs.

ine eggs that 88% (1 of every 1.1 eggs) of cowbird eggs were misclassified as belonging to another species (Table 2). Between 8 and 48% of cowbird eggs were misclassified depending on the grassland hosts, when compared to eggs of each species separately (Table 3). Thus, any cowbird egg laid randomly in a Sprague's Pipit, Vesper Sparrow, Savannah Sparrow, Baird's Sparrow, or Chestnut-collared Longspur nest has between a "one-in-three" and a "one-in-two" chance of matching the hosts eggs; the chance of matching for Western Meadowlarks is significantly lower at approximately "one-in-ten" (Table 3). Effective mimicry requires most cowbird eggs to match the eggs of at least one host. This is especially true considering female cowbirds are thought to exhibit little to no host selection (Fleischer 1985, Alderson et al. 1999). "Generalized" mimicry necessitates that color and maculation density of cowbird eggs overlap to a significant extent with the eggs of all six species.

Another important component of generalized mimicry is the idea that a single cowbird egg may mimic the eggs of more than one species. This contrasts with the elaborate mimetic system evolved by the Common Cuckoo. Different subgroups or "gentes" of female cuckoos in that system mimic the eggs of a preferred host (Davies and Brooke 1988, Marchetti et al. 1998, Gibbs et al. 2000). The benefit of gentes is that it allows cuckoos, as a species, to parasitize several species that exhibit egg discrimination while lowering competition for nests (Davies and Brooke 1988). Cowbird gentes are supported (Fig. 1), illustrating some of the remarkable similarities we discovered between cowbird eggs and the egg of each grassland passerine. However, the high frequency at which cowbird eggs were misclassified when compared to the eggs of each species (8 to 48%, sum total 186%; Table 3) is only possible if individual cowbird eggs are capable of matching the eggs of more than one species. We conclude that eggs of individual female cowbirds have not evolved to mimic those of a preferred species.

Cowbird eggs were more evenly maculated than the average grassland passerine egg despite the strong resemblance in three of four parameters (Table 1). This discrepancy may arise because an unforeseen cost exists for cowbird eggs that are more unevenly maculated, e.g., increased rates of depredation (Underwood and Sealy 2002, Kilner 2006). Cowbird eggs have similarly been shown to be rounder than host eggs to increase shell strength and reduce the potential for damage during laying or by intolerant hosts (Rohwer and Spaw 1988, Picman 1989). Alternatively, divergences in maculation distribution might reflect the parameters used by grassland passerines to discriminate cowbird eggs. Rothstein (1982) found that Gray Catbirds (*Dumetella carolinensis*) were more responsive to changes in color than maculation, and American Robins (*Turdus migratorius*) were more sensitive to color than size (also Underwood and Sealy 2006). Differences in

host discrimination alter the selective pressure placed on cowbird eggs by each host and modify which parameters are mimicked (Rothstein 1982, Underwood and Sealy 2006). Consequently, the distribution of maculation may not be imitated by cowbirds because grassland passerines discriminate foreign eggs solely on the basis of color and density of maculation.

Our results show that cowbird eggs were most readily distinguished from eggs of Western Meadowlarks on the basis of color and maculation density (Tables 2, 3). This corresponds with the level of intolerance observed for this species compared to the other five grassland passerines (Klippenstine and Sealy 2008). Western Meadowlarks ejected 67% of cowbird eggs and 91% of the non-mimetic eggs added to their nests. The five remaining grassland passerines, in comparison, accepted all or nearly all cowbird eggs and ejected about 20% of non-mimetic eggs (Klippenstine and Sealy 2008). Western Meadowlarks apparently eject cowbird eggs more readily because of the lower extent of matching between the eggs of the two species. Peer and Sealy (2004) rated Western Meadowlarks eggs similar in color and maculation to cowbird eggs. They also suggested egg appearance was not correlated with this host's intolerance of parasitism, but was related to their larger beaks. We suspect the difference arises because they compared the color and maculation of eggs using human observers. It is extremely difficult, however, for a human observer to assess the density of maculation independent of its distribution, which in this study had a profound affect. Consequently, discrepancies observed between the two studies emphasize the benefits of assessing egg appearance quantitatively.

Generalized cowbird egg mimicry is not the only possible explanation of the close resemblance between cowbird eggs and grassland passerine eggs. Concealment of eggs in the nesting habitat from depredation is a primary force directing the evolution of egg appearance in most species (Underwood and Sealy 2002, Kilner 2006). Therefore, the same forces promoting the evolution of color and maculation density in grassland passerine eggs may have selected the same pattern in cowbird eggs (Underwood and Sealy 2002, Kilner 2006). We propose two criteria to distinguish between resemblance due to nest concealment and cowbird egg mimicry. The first is that cowbird egg mimicry requires host species that exhibit egg discrimination and ejection. The presence of egg discrimination in all six species strongly supports the idea of cowbird egg mimicry (Klippenstine and Sealy 2008). A worthwhile test of this criterion would be to examine the extent of matching between cowbird eggs and eggs of grassland passerines that have not evolved egg recognition. The second criterion is that nest concealment would not necessarily make cowbird eggs better at matching grassland passerine eggs than eggs of any other grassland passerine. That cowbird eggs were significantly more likely to be misclassified than all other grassland passerine eggs (88% vs. 4–70%) supports generalized cowbird egg mimicry (Table 2).

The benefits of mimicking grassland passerine eggs are obvious for cowbirds. Despite having evolved egg discrimination, all six grassland species fully or partially accept cowbird eggs (Davis et al. 2002, Klippenstine and Sealy 2008). This tolerance has translated into reasonable breeding success for cowbirds within this community (Davis et al. 2002, Davis 2003, Klippenstine and Sealy 2008).). However, we believe the value of generalized cowbird mimicry is most likely limited to only a few host assemblages. Communities where host eggs are highly divergent in appearance are probably not conducive to generalized mimicry (Rothstein 2001). Generalized cowbird egg mimicry, even for grassland passerines examined in this study, is feasible only because each host exhibits a relatively crude level of egg recognition (Klippenstine and Sealy 2008). Greater selective pressure will be placed on cowbirds to evolve more species-specific egg mimicry as continued parasitism forces grassland passerines to develop their ability to discriminate foreign eggs (Moksnes et al. 1990, Davies and Brooke 1991). Cowbird egg mimicry of grassland passerine eggs may eventually resemble the type of mimicry exhibited by the Common Cuckoo. Alternatively, as Rothstein (2001) suggested, cowbirds may in the future choose to avoid such troublesome hosts.

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FLIGHT FEATHER MOLT OF TURKEY VULTURES

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ABSTRACT.—We document the molt sequence of flight feathers in Turkey Vultures (*Cathartes aura*) based on studies of captive and wild birds, and examination of museum specimens. We found an unusual pattern of primary replacement, which appears to be a modified form of *Staffelmauser*, or stepwise wing molt. A *Staffelmauser*-like strategy for replacement of the secondaries is also described. These patterns of feather replacement appear to be adaptations to maintain flying performance while replacing all primaries and most secondaries during each molt. To what extent molt patterns in Turkey Vultures reflect convergent adaptation for flight, rather than ancestral characters useful for phylogenetic studies, remains unknown. *Received 15 June 2009. Accepted 12 January 2010.*

Maintaining optimal flight performance is essential for Turkey Vultures (*Cathartes aura*), a species adapted for long-term soaring (Rosser and George 1986, Tucker 1987). This species locates its primary diet of carrion by detecting odor plumes while aloft, and spends most daylight hours searching for food (Owre and Northington 1961, Stager 1964). It is a migratory species that can travel hundreds or thousands of kilometers seasonally between southern wintering and northern breeding areas (Stewart 1977, Kirk and Houston 1995, Bildstein and Zalles 2001).

Little is known about the molt of Turkey Vultures despite its widespread distribution and abundance (Kirk and Mossman 1998). Identifying and understanding molt processes in birds can be accomplished in several ways. Miller (1941), Stresemann (1963), and Pyle (2005) used data from museum study skins of raptors to make their basic molt sequence hypotheses. Analyzing molt patterns from study skins can be difficult and may not represent the progression of a single individual, and sample sizes of large birds are typically too low to undertake comprehensive analyses. Houston (1975) observed flight feather replacement in both captive and wild individuals of Old World vultures (*Gyps*), but molt in captive birds may not reflect that of wild birds (*cf.* Pyle 2005). Snyder et al. (1987) based their molt study of California Condors (*Gymnogyps californianus*) on photographs of wild birds in flight. Bloom and Clark (2001) used banding records with some recaptures to study the molt of the Golden Eagle (*Aquila chrysaetos*), but sample sizes of known individual birds are low in these studies. Ideally, a complete understanding of molt strategies would be based on the study of wild birds, captive individuals, and specimens; we present such an analysis of molt in Turkey Vultures.

METHODS

A. M. Rea began collecting molt sequence data on Turkey Vultures in 1972 as part of a larger study on the phylogenetic relationship of New World vultures (Rea 1983). Chandler joined the project in 1978, collecting feathers from three adult individuals held captive at the San Diego Natural History Museum (SDNHM) in San Diego, California, USA and studying molt year-round on several others. Flannery and Long tabulated molt data on five vultures (4 adults and 1first year bird) between 2002 and 2004, which were held captive by the California Academy of Sciences (CAS) in San Francisco, California. The extended study period of captive individuals allows calculation of feather replacement rates both within and between individuals to establish ranges of variation. Pyle and Howell visually examined hundreds of vultures in the field, and Pyle and Flannery examined molt in over 20 museum specimens.

We classified ages of Turkey Vultures using head and beak coloration (Henckel 1981), and known history for captive individuals. Age coding of birds follows Pyle (1997): HY (hatching or first calendar year), SY (second calendar year), TY (third calendar year), and ASY (at least third

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calendar year). Chandler collected data from two captive (SDNHM) ASYs during 1972–1980 and a third ASY during 1979–1980. Flannery and Long collected data from four captive ASYs (3 males and 1 female known to be ages 7+ to 25+ years) and a female received as an HY, housed at CAS during 2002–2004. The ASYs were from Oklahoma, Pennsylvania, and Texas; the HY, received with down still present on the head and the majority of the beak still dark, was from Tennessee and arrived in December 2001. All eight individuals were kept in outdoor pens, ensuring they were acclimated to the natural local photoperiod and climate.

Primaries, secondaries, and rectrices for the vultures studied by Chandler (SDNHM) were painted with a dot and slash code to identify the specific feather (a dot = 1 and a slash = 5), and with a year-specific color for each individual for each year of study. The aviary was checked several times daily for dropped feathers, which were labeled and dated. Wings were examined visually for the individuals at CAS, and dropped feathers were examined to tabulate wing molt data. Primaries and secondaries on each healthy wing of each individual were scored as old, missing, in pin, growing, or new. The percentage of feather length grown was recorded for each growing feather. Data were collected weekly during the first year of the study and biweekly or monthly in subsequent years. Drop dates for each primary on each bird were estimated by calculating primary-specific growth rates and obtaining mean, back-calculated dates for each feather. Feathers not dropped that year were designated as being retained in both studies.

Pyle and Howell recorded data from 1998 to 2006 on wing molt from Turkey Vultures in the field. Binoculars were used to score primaries as missing, growing, new, or old. Molt was assumed if the same primary was missing or growing on both wings simultaneously; individuals with a missing or growing primary on only one wing were not included in the data set. Data were collected year-round and, although most data were obtained from central California, at least 10 birds each from Maryland, Indiana, Mexico, and El Salvador were scored. Vultures observed with dark heads and beaks, and no primary molt in June-December were classified as HYs and not included in the data set. Analysis was based on date of observation and progression of molt, including either no molt, or a score representing the number of the primary that was growing on the observation date. Individuals with two primaries being replaced simultaneously from different parts of the wing (e.g., an inner and an outer primary) were scored twice in the data set. Secondary molt patterns also were scored when visible. We analyzed the data using a two-tailed *t*-test with JMP Version 5.1 statistical software (SAS Institute 2002) to examine whether or not there was a difference in mean dates of molt between captive and wild birds.

More than 20 specimens at CAS, Museum of Vertebrate Zoology (MVZ), SDNHM, and the National Museum of Natural History (USNM) were examined. Primaries and secondaries were scored in the same manner as captive birds, and replacement sequences were inferred based on wear clines reflecting protracted molts (Pyle 2005).

RESULTS

Primaries.—All data indicate the 10 primaries of a Turkey Vulture molt sequentially from the innermost primary (P1) to the outermost primary (P10). This process started for the SY at CAS in late January with P1 and was completed in late July with P10 (Fig. 1). This SY then replaced P1–P3 for a second time within the year in September–November (Fig. 1). The following year, as a TY, this individual continued the sequence where it had suspended the year before, replacing P4–P10 in order between early March and early August, and replacing P1–P3 in August–September (Fig. 1). The captive ASYs at both locations replaced P5–P10 in March–September and replaced P1–P2 in July–August (Fig. 1). This pattern averaged later than the drop dates recorded for the younger bird as an SY and a TY. Replacement of P3 and P4 in ASYs was more variable (Fig. 1).

Based on the above results, data on P1–P4 from birds in the field were partitioned as either molting in August–November or in January–March (Fig. 2). The remaining primaries, P5–P10 had sequential mean dates of molt, beginning in April–May (P5) and finishing in September–October (P10). This pattern was similar to that recorded for captive birds of all ages (Fig. 2). Mean dates of molt for P1–P4 and P7–P8 were not significantly different between captive and wild birds. However, mean drop dates were significantly earlier (two-tailed *t*-test, $P < 0.01$) in

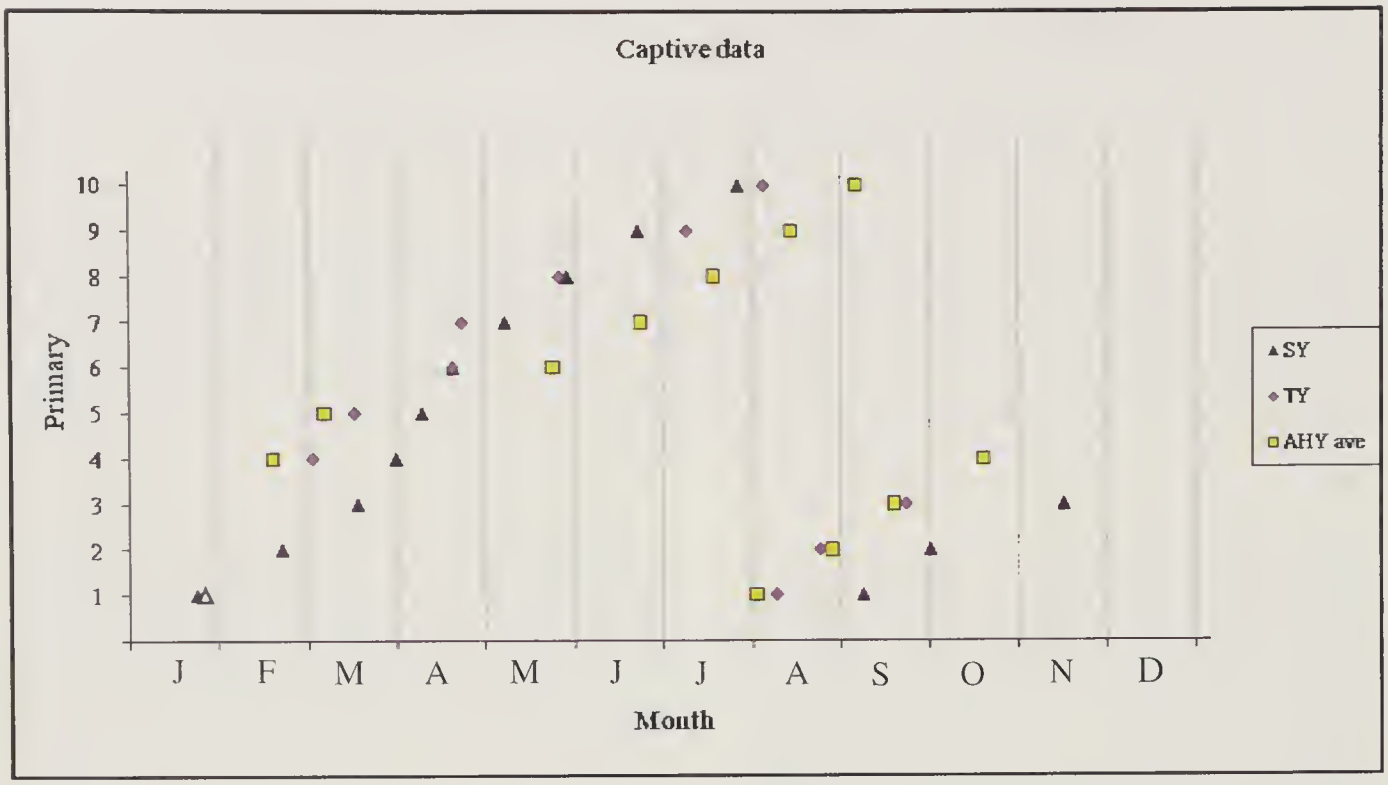

FIG. 1. Calculated feather drop date by month for Turkey Vultures. Data collected from Turkey Vultures held captive at the California Academy of Sciences. SY and TY data collected from same individual during 2002 and 2003. Open triangle represents assumed drop date for P1 in a SY calculated using percentage feather grown; actual drop date occurred prior to acquisition of the bird.

captive than in wild populations for P5, P6, P9, and P10. This difference is most likely attributable to the higher energy requirements for breeding and food acquisition observed in wild populations that could suspend, slow down, or otherwise delay molt.

Three vultures observed in the field were replacing P1 during 20–29 January. All three

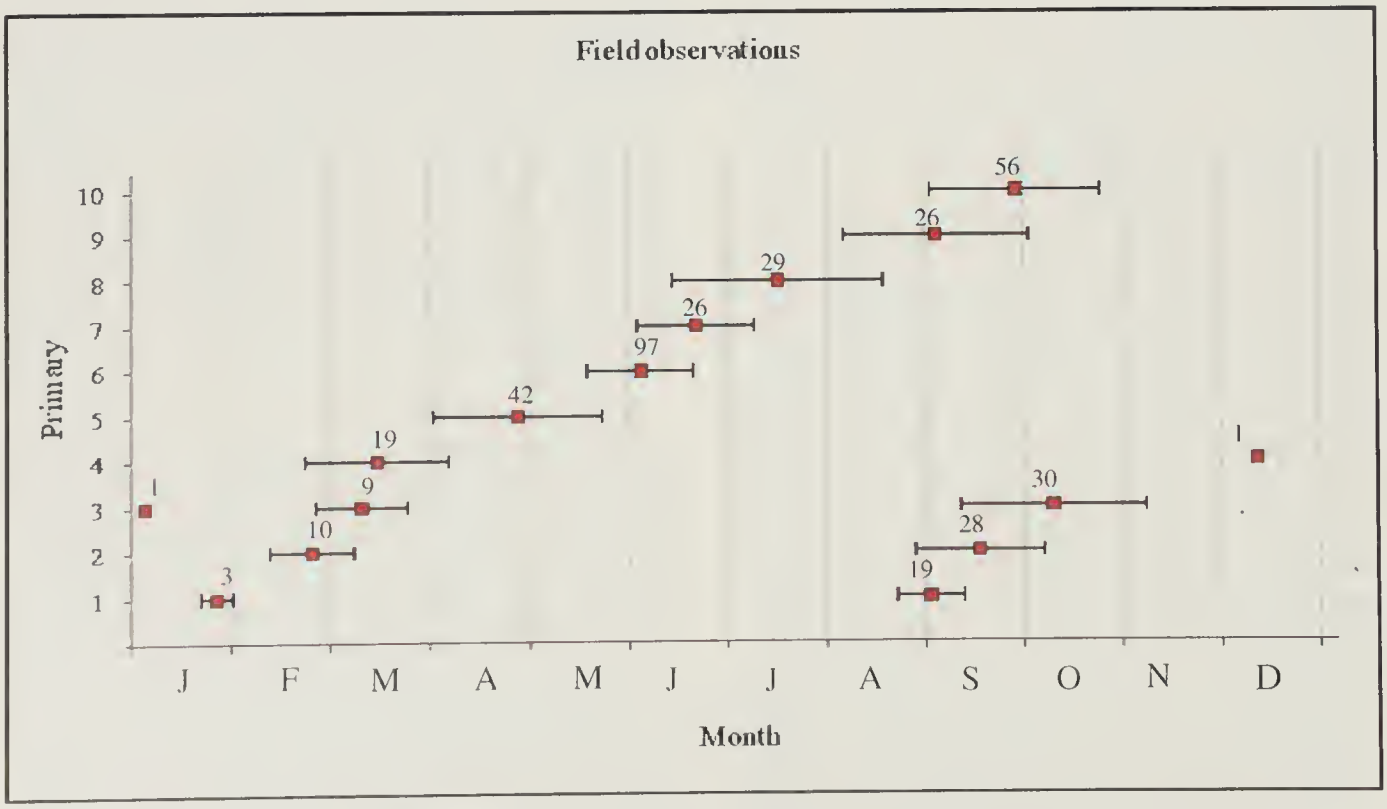

FIG. 2. Mean (± SE) feather drop date for Turkey Vultures by month based on field observations.

were classified as SYs by head plumage and evenly worn primaries (P2–P10). Most of 19 vultures observed replacing P2–P3 in February and March (Fig. 2) were classified as SYs. In contrast, many of the 77 vultures observed replacing P1–P3 in August–November (Fig. 2) were ASYs. Vultures replacing P4 in February–April (n = 19) included three SYs and seven ASYs. Two vultures that could not be partitioned into our defined categories were replacing P3 on 4 January and P4 on 7 December (Fig. 2). Both of these individuals were observed in central California. ASY vultures showing no primary molt (n = 181) were observed between 6 September and 17 March. The mean (± SD) date for individuals showing no molt was 14 January ±49 days.

Secondaries.—There were three consistent foci for initiating molt of secondaries based on data from the SDNHM captive birds, specimens, and field observations: the tertials and secondaries 1 and 5 (S1 and S5, numbered proximally from outermost). Molt proceeded proximally from S1 and S5 and distally from the tertials, and it may become irregular in the area from S8 to S11. Six secondaries were retained from 1973 to 1978 on captive ASYs (SDNHM), two for one bird and four for the other individual. Combined locations of retained secondaries for the two birds were: S4, S7 (twice), S8 (twice), and S10. S1 dropped regularly in April followed by S2 and S5 in May and June, respectively. S3 and S6 usually dropped in June, S4 and S7 in July, S8 in August or September (but at times as early as mid-July), and S9 and S10 dropped between June and late September; S9 always dropped before S10. There was a tendency for molt to terminate at S11 and S12 with drop dates between May and June, and S12 following S11. Smaller secondaries (S1–S4) dropped together in April and May and as late as August. The tertiary feathers, as with the smaller secondaries, had a tendency to drop together between May and August with no discernable sequence.

There appeared to be some interannual variation in the number of secondaries retained. For example, 1979 was an atypical year of extraordinarily high numbers of retained feathers. One vulture retained five secondaries and two rectrices, another had nine secondaries and one rectrix retained that year. A possible reason is that the birds suffered from lead poisoning. The following year, after the birds had recovered from the apparent lead poisoning, no feathers were retained. Retained feathers dropped in May or June of the next year.

Rectrices.—Tail feathers generally had a consistent pattern for the six feather pairs (SDNHM). On one side, numbering rectrices from the central feather R1 to the outermost feather R6, the sequence was R1-R6-R2-R4-R3-R5. R1 dropped between late April and May, R6 dropped regularly in May. The largest rectrix, R2, dropped in late May or June, followed by R4 in late June or July, R3 in July or August, and R5 in mid-August to early September. Tail feathers retained from the previous year dropped in May or early June of the next year. Three rectrices were retained during the first 6 years (1973–1978), a pair of R4s for one vulture and a single R5 for another.

Feather Synchrony and Growth.—Time elapsed between dropping of paired (right and left) feathers was calculated for P5 in captive birds at SDNHM. The average elapsed time was 7 1/2 days after the first of the pair had dropped (range 1–41 days). P1 and P6 through P10 held to this average or had an even shorter elapsed time, at times less than 24 hrs. P2 through P4 had the greatest range with an average of less than 10 days for P2 to an average of 1 month for P3 and P4. The maximum time for an individual feather was 41 days between drop dates for P3.

DISCUSSION

Basic concepts of flight feather molt in diurnal soaring hawks, eagles, and Old World vultures have been presented by Miller (1941), Stresemann (1963, 1966), and Stresemann and Stresemann (1966). Later studies on wing molt by Brown and Amadon (1968), Houston (1975), Brown (1976), Edelstam (1984), Clark (2004), and Pyle (2005) have led to hypotheses about the role of flight feather replacement schemes that may be used to infer possible differences in flight strategies and aerial performance. Birds molt for specific reasons during certain times of the year and this molt is not random feather loss, but has a definite sequence that has an adaptive advantage in optimizing aerodynamics with respect to feather maintenance (Hedenstrom and Sunada 1999, Rohwer 1999, Pyle 2006).

Large birds exhibit several remigial replacement strategies detectable within a year and between years by wear patterns, contrasting feather appearance, and retained feathers (Pyle 2005, 2006, 2008). The most common strategy of molt among large birds that need to maintain

flight, involves a *Staffelmauser* pattern meaning "staggered molt" (Stresemann and Stresemann 1966) and also known as "stepwise molt". Falconids typically replace all primaries and secondaries during each prebasic molt using multiple waves originating at P4 and S4, whereas larger accipitrids can retain primaries and secondaries from a previous season as part of a *Staffelmauser* sequence (Pyle 2005). The physiological demands of producing new feathers and the time required to complete a full molt are correlated to body mass and efficiency for flight requirements of larger birds (Shugart and Rohwer 1996, Pyle 2005). Sequential replacement of feathers in waves without having large gaps, increases the efficiency of wings and still allows larger birds to fly. A *Staffelmauser* pattern occurs in a wide range of larger birds, e.g., pelicans, herons, and condors (Pyle 2006, 2008).

As widespread and common as Turkey Vultures are throughout the Western Hemisphere, it is surprising that no comprehensive review has been published about their molt (but note comments and references by Kirk and Mossman 1998). For example, Stresemann and Stresemann (1966) mentioned that primaries are replaced irregularly, but Jackson (1988) correctly reported that, barring some aberrant irregular patterns, the molt takes place annually and within a single year, being replaced in a serial inner-to-outer sequence. Rea (1983) included findings by Chandler on secondaries and rectrices.

Our data produce a clearer picture of the flight feather molt of Turkey Vultures, which show similarities to other New World vultures, and the California Condor (Snyder et al. 1987). However, the molt of Turkey Vultures is more regular, more symmetrical between wings, and in a 1-year rather than the condor's 2-year cycle. There have been no comprehensive studies published on other cathartid vultures for additional comparisons or differences in molt in the Cathartidae.

Further comparisons of flight feather molt with other species of birds can be made in two ways, either by comparing molt in avian families related to the Cathartidae, or by comparing molt adaptations in other avian families that show morphological convergence with soaring flight. Unfortunately, the proximate affinity of cathartid vultures to other avian groups (e.g., Falconiformes or Ciconiiformes) remains unresolved (Ligon 1967, Rea 1983, Emslie 1988, Sibley and Ahlquist 1990, Avise et al. 1994, Helbig and Seibold 1995, Wink 1995, Livezey and Zusi 2007). The wing molt of Turkey Vultures, depending on phylogenetic relationships, may reflect an ancestral pattern. Molt patterns similar to those in Turkey Vultures are shared by some species of Ciconiiformes (Bloesch et al. 1977, Shugart and Rohwer 1996), a proposed ancestral group to Cathartidae. However, similarities in molt patterns are also seen in several other taxonomic groups, and are considered to be a widespread convergent molt adaptation in many taxa of larger soaring birds (Pyle 2006). Further data are needed to address this nature versus nurture issue.

Molt Terminology.—Turkey Vultures have an unusual pattern of primary replacement (Figs. 1, 2) that could be interpreted in several ways. One interpretation would be that the second molt cycle of SY birds involves replacement of P1–P3 (occasionally P1–P4) twice. This would necessitate labeling one of the replacements, either that of January–March or that of August–November, as a prealternate molt. Each successive prebasic molt typically would then begin at P4 (or P5) in the spring and finish with P1–P3 (or P1–P4) in the fall. However, prealternate molts are not known to occur among families thought to be close relatives of New World vultures.

A second interpretation would be that replacement of P1–P3 in SYs in the fall represents an advanced start to the third prebasic molt, concurrent with completion of the second prebasic molt. Each subsequent prebasic molt would then begin with P1 in the fall, usually (but not always) suspend for the winter, and resume with P4 in the spring (Pyle 2008). This is essentially a modification of *Staffelmauser*, in that all primaries are replaced in 1 year via two waves. Incomplete-to-complete replacement of the secondaries also appears to follow a *Staffelmauser*-like strategy found in other large birds (Pyle 2006). However, molt of primaries differs from text-book *Staffelmauser* in that replacement of P1 in the second wave is delayed until after the preceding wave has replaced the middle primaries; the molt assumes an annual regularity not found in other species exhibiting *Staffelmauser*. The advancement of some or all primary molt in selected species of a family, to occur before another life-history event (migration, breeding, chick-feeding), has been documented among loons, puffins, gulls, and diurnal raptors (Howell 2001, Howell and Pyle 2005, Pyle 2005). However, in these groups the second prebasic wing molt typically occurs or

starts *later* in SYs than in subsequent ages, which is not the case in Turkey Vultures.

A third interpretation would be to treat the first wing molt of Turkey Vultures as a preformative molt and the molt of P1–P3 of SYs in the fall as the start of the second prebasic molt. The idea of a preformative molt being limited to flight feathers has not previously been recognized, but Howell (in press) has argued that *Staffelmauser* can develop in two ways. One is the conventional view that the first wing molt pertains to the second prebasic molt (a normal schedule), the other is that the process of *Staffelmauser* is kick-started by insertion of a preformative wing molt (an accelerated schedule). Species exhibiting accelerated schedules include Osprey (*Pandion haliaetus*), and most if not all Pelecaniformes (Howell, in press). The first wing molt in these species starts earlier than subsequent wing molts, which is also true of Turkey Vultures. To what extent normal and accelerated schedules reflect ancestral traits or environmental responses remains unknown.

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The First Reported Case of Cooperative Polyandry in the Red-footed Booby: Trio Relationships and Benefits

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ABSTRACT.—We report the first observations of cooperative polyandry in the Red-footed Booby (*Sula sula*), a trio that remained stable over at least 4 consecutive years. Both males were heterosexual; neither was dominant. One male was more sexually active, but mounting activity suggested shared paternity over the years. Trio males, compared to monogamous males, invested more in pair bond maintenance activity which possibly assisted in maintaining a stable breeding unit. Trio members, like monogamous adults, shared breeding duties evenly, reducing the total investment for each trio member relative to that of monogamous adults. The extra foraging effort of the trio enabled similar provisioning rates in good and bad years. We suggest trio formation improved female lifetime reproductive success due to enhanced nest, egg, and chick care; maintained stable food provisioning rates despite highly heterogeneous foraging conditions; and increased male survivorship due to sharing of breeding duties. Red-footed Booby trio formation is probably an "opportunistic deviation" from normal monogamy which is favored by differential costs and benefits to males and females. *Received 15 July 2009. Accepted 10 January 2010.*

Most seabirds are monogamous (Lack 1967), i.e., cooperative mating systems are rarely observed and there is little information on parental investment or cost and benefits to the individuals involved (Stacey and Koenig 1990, Phillips 2002, Ludwigs 2004). Brown Skuas (*Stercorarius antarcticus*), forming polygynous and polyandrous trios, were no more reproductively successful than monogamous pairs (Phillips 2002). A Common Tern (*Sterna hirundo*) trio raised more chicks than comparable monogamous pairs through higher brooding and provisioning rates (Ludwigs 2004).

The Red-footed Booby (*Sula sula*) is socially monogamous showing reversed sexual size dimorphism (Nelson 1978); both adults share parental duties equally (Weimerskirch et al. 2006). We report the first description of cooperative polyandry in the Red-footed Booby, a trio that nested five times in the same tree during 2004–2007. We studied trio male bond maintenance activities and breeding behavior to test whether trio members shared parental duties as in monogamous pairs.

METHODS

Study Site and Field Work.—Dong Island (16° 40′ 03″ N, 112° 43′ 52″ E) is in the northern South China Sea and supports ~35,500 pairs of Red-footed Boobies (Cao 2005). A trio nested five times during 2004–2007: in March 2004, January 2005, November 2005, December 2006 (when all nests in the colony were destroyed by a typhoon), and March 2007. Trio male bond maintenance behavior during the nest-building period was observed for 115 hrs in 2006 and 124 hrs in 2007, standardized to 100 hrs for analysis. The trio and four adjacent monogamous nests (pair numbers: N9, N11, N12, and N13) were studied in 2007 from nest building to chick fledging to compare adult behavior. Nest construction started between 6 and 19 March and chicks fledged from 17 to 23 August. Observation periods/breeding durations of the five nests were: trio = 893 hrs/169 days; N9 = 873 hrs/164 days; N11 = 874 hrs/167 days; N12 = 880 hrs/166 days; and N13 = 803 hrs/158 days; activities were standardized to 1,000 hrs for analysis (heterosexual mounting was standardized to 100 hrs). Age of birds was classified based on plumage (Nelson 1978) and males and females were classified using color of bare facial parts (James 2001) and voice (Lormée et al. 2003). Trio individuals were uniquely color marked. Measurements were taken of the trio and paired adults following Lowe (1989).

Studies of breeding behavior focused on bond maintenance and division of labor. Bond maintenance was measured as frequency of sexual activities (sky-pointing and mounting) and mate preening per unit of time. Division of labor included nest attendance (% time spent by each

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TABLE 1. Trio male bond maintenance activities during nest building in 2006 and 2007. Values rounded to the nearest whole number for clarity of presentation; NS = not significant ($P > 0.05$).

	2006			2007			2006 vs. 2007	
Activity (n/100 hrs)	♂A	♂B	♂A vs. ♂B	♂A	♂B	♂A vs. ♂B	♂A	♂B
Sky-pointing	4	17	$P < 0.01$	2	31	$P < 0.001$	NS	$P < 0.05$
Heterosexual mounting	23	43	$P < 0.05$	23	16	NS	NS	$P < 0.001$
Homosexual mounting	3	10	$P < 0.05$	2	5	NS	NS	NS
Heterosexual preening	30	10	$P < 0.001$	32	13	$P < 0.01$	NS	NS
Homosexual preening	17	4	$P < 0.01$	24	9	$P < 0.01$	NS	NS

adult), territorial defense (frequency of flight-circuiting, fighting, wing-flailing, and forward head waving; Nelson 1978), nest construction (frequency of delivery of nesting material by each bird), incubation (hrs spent by each adult; data were standardized to 300 hrs for analysis), provisioning and foraging; provisioning was measured by the percentage of days that: (1) each adult fed the chick, and (2) foraging trips were undertaken by each adult during the observation period. Provisioning and foraging data collection occurred during the late chick-rearing period after brooding ceased.

Chicks were weighed at 0700, 1600, and 2000 hrs daily from 60 to 88 days after hatching (peak body mass period before fledging; Cao 2005) to learn whether they had been fed and the amount of food delivered (calculated as the difference between successive weighings).

Breeding success (fledglings produced divided by the number of eggs laid) was calculated for the trio and the general population by checking nests every 5 or 10 days. Data affected by the super typhoon in December 2006 were omitted from the calculation, as a typhoon of this strength, which destroyed all nests in the colony, is a rare occurrence (about once every 20 years).

Statistical Analyses.—The binomial distribution was used to examine differences between activity levels of trio individuals and between those of trio and monogamous individuals (Tables 1, 2) using the equation: $z = |p - 0.5|/\sqrt{\{\mathrm{Var}(p)\}}$ based on the null hypothesis that a p-value of 0.5 is expected if there is no difference between activity levels (p = proportion of the combined activities attributable to one individual and $\mathrm{Var}(p) = p(1 - p)/n$ [n = combined activities of the 2 individuals]).

We calculated the number of standard deviation units (z) that the activity level of the trio member (x) was from the mean activity level of the monogamous sample ($\bar{x}$) using the equation $z = (x - \bar{x})/s$, where s = standard deviation for the monogamous sample, to examine differences between division of labor activity levels of trio and monogamous pair individuals (Table 2).

We used the z-score for sample sizes greater than 30, and the t-distribution for smaller sample sizes (Fowler and Cohen 1996); all tests were two-tailed. The t-test was used to examine differences between adult measurements (mass, wing length, etc) and between food deliveries to chicks. Data are presented as mean ± SD.

RESULTS

Measurements.—The trio consisted of adult males ♂A and ♂B, and an adult female (♀A). Body masses of ♂A (948 g) and ♀A (961 g) were similar, ~ 10% heavier than ♂B (856 g), but body masses of trio members were not different ($P > 0.05$) from those of paired adults (male = 852 ± 47.1 g, n = 17; female = 956 ± 77.9 g, n = 14); differences were not significant ($P < 0.05$) between culmen lengths (♂A = 84.0 mm; ♂B = 85.5 mm; ♀A = 85.0 mm; paired adults: male = 82.7 ± 2.64 mm, n = 17; female = 84.7 ± 2.94 mm, n = 14) or wing lengths (♂A = 386 mm; ♂B = 373 mm; ♀A = 377 mm; paired adults: male = 377 ± 8.1 mm, n = 17; female = 382 ± 5.9 mm, n = 14).

Breeding Behavior.—Trio males were heterosexual (Table 1); no agonistic behavior was observed, even when both males were present during copulation and sky-pointing. Male A mate-preened significantly more and ♂B sky-pointed significantly more in both years, but ♂B did significantly more mounting than ♂A in 1 year. Male A exhibited similar bond maintenance behavior in both years, but ♂B sky-pointed significantly more and did less heterosexual mounting in 2007. The trio indulged in far more bond maintenance activity than monogamous pairs, but frequency of heterosexual mounting was not significantly different (Table 2).

TABLE 2. Breeding behavior of trio and monogamous pair members during nest building to chick fledging in 2007. Values rounded to the nearest whole number for clarity of presentation; trio male duplicate data are for ♂A and ♂B, respectively; NS = not significant ($P > 0.05$).

		Trio	N9	N11	N12	N13	*P*
Sky-pointing (*n*/1,000 hrs)	Male(s)	5/48	0	10	8	0	NS/$P < 0.01$
	Female	0	1	0	0	0	
	Total	53	1	10	8	0	$P < 0.01$
Heterosexual mounting (*n*/100 hrs)	Male(s)	23/16	23	34	30	14	NS/NS
	Total	39	23	34	30	14	NS
Mate preening (between sexes) (*n*/1,000 hrs)	Male(s)	139/36	2	17	0	25	$P < 0.01$/NS
	Female	3/10	12	13	0	44	NS/NS
	Total	188	14	30	0	68	$P < 0.05$
Nest attendance (hrs/1,000 hrs)	Male(s)	384/486	397	311	372	408	NS/NS
	Female	411	404	488	371	467	NS
	Total	1,281	801	800	743	875	$P < 0.01$
	♂/♀ ratio	30:38:32	50:50	39:61	50:50	47:53	NS
Territorial defense (*n*/1,000 hrs)	Male(s)	184/258	111	114	119	93	$P < 0.01$/$P < 0.01$
	Female	110	136	135	98	103	NS
	Total	551	247	249	217	197	$P < 0.01$
	♂/♀ ratio	33:47:20	45:55	46:54	55:45	47:53	NS
Nest construction							
Nest material supply (*n*/1,000 hrs)	Male(s)	82/78	235	237	256	54	NS/NS
	Female	1	6	1	2	3	NS
	Total	161	241	238	258	56	NS
Nest building (*n*/1,000 hrs)	Male(s)	24/27	13	5	8	5	$P < 0.05$/$P < 0.05$
	Female	108	192	212	240	44	NS
	Total	159	205	217	248	49	NS
Totals	♂/♀ ratio	33:33:34	56:44	53:47	52:48	56:44	NS
Incubation (hrs/300 hrs)	Male(s)	69/89	125	118	151	137	$P < 0.05$/NS
	Female	142	175	182	149	163	NS
	♂/♀ ratio	23:30:47	42:58	39:61	50:50	46:54	NS
Provisioning							
Days chick fed by each adult (%)	Male(s)	89/21	62	77	56	69	NS/$P < 0.05$
	Female	39	86	59	67	46	NS
	♂/♀ ratio	60:14:26	42:58	57:43	46:54	60:40	NS
Foraging							
Days foraging trips made (%)	Male(s)	100/86	95	100	100	100	NS/$P < 0.05$
	Female	96	100	95	94	92	NS
	♂/♀ ratio	35:31:34	49:51	51:49	52:48	52:48	NS

Trio members shared nest attendance, total nest construction, and foraging activities evenly, except ♂A did more provisioning and less incubation, ♂B conducted more territorial defense and less provisioning and foraging, and both males did more nest building than monogamous pairs. Trio members shared parental duties equally, which reduced individual contributions to nest construction, incubation, and provisioning while enhancing nest attendance, territorial defense, and foraging effort through the presence of an additional adult.

Food Delivery and Breeding Success.—Significantly more food was delivered to chicks of monogamous parents in 2007 compared to 2004 (2007: 3,744 ± 371 g, $n = 6$; 2004: 2,837 ± 95 g, $n = 3$; $P < 0.05$) because adults delivered food on a greater percentage of days (2007: 97 ± 2.2%, $n = 6$; 2004: 75 ± 3.5%, $n = 3$, $P < 0.05$). The trio delivered significantly more food in 2004 than the average monogamous pair (3,485 g vs. 2,837 ± 95 g, $n = 3$, $P < 0.05$) as they fed their chick on a significantly higher percentage of days (97% vs. 75 ± 3.5%, $n = 3$, $P < 0.05$).

Monogamous pairs in 2007 delivered more food than in 2004 because foraging conditions were better. The trio overcame poor feeding conditions in 2004 due to their combined foraging effort which maintained food delivery at a similar level in both years (2004: 97%; 2007: 96%). Excluding the typhoon year, the trio successfully fledged four chicks, i.e., one chick/year, compared with 0.49 (n = 35) chicks/year in the general population.

DISCUSSION

Trio Relationships.—Measurements and body mass suggested trio members were not the result of associations between poor quality individuals. Male A adopted the female position more often during homosexual mounting in one of the years, but its overall sexual behavior was similar to that of monogamous males. Trio members, like monogamous adults (Weimerskirch et al. 2006), shared breeding duties equally, but males indulged in more bond maintenance than monogamous males (especially ♂A), which may have contributed to maintaining trio stability over 4+ years, as suggested by Gonzalez et al. (2006) for the Spanish Imperial Eagle (*Aquila adalberti*). Neither trio male seemed dominant, consistent with "type one" cooperative polyandry of Heinsohn et al. (2007) where males share territorial defense and are non-aggressive towards each other.

Benefits of Being a Trio.—Breeding success for the trio female was double that of monogamous females, similar to observations of Common Terns (Ludwigs 2004), and Galapagos (*Buteo galapagoensis*) and Harris' hawks (*Parabuteo unicinctus*) (Faaborg and Bednarz 1990), but male productivity did not differ. Suggested reasons for increased trio individual lifetime reproductive success (Phillips 2002, Ludwigs 2004, Gonzalez et al. 2006) also apply to the Red-footed Booby trio:

(1) enhanced nest, egg, and chick care from three adults;

(2) stable food delivery in an heterogeneous environment (Weimerskirch et al. 2005): the extra foraging adult maintaining similar food provisioning rates in good and bad seasons may be adaptive in dynamic environments (Rubenstein and Lovette 2007);

(3) enhanced survival: sharing of breeding duties between trio members particularly benefits males which lose body condition late in the chick-rearing period (Lormée et al. 2003, Weimerskirch et al. 2006).

Why Aren't There More Trios?—Assuming a random sample, observations of 54 Dong Island nests suggested that cooperative polyandry was rare, occurring at <2% of Red-footed Booby nests. This is surprising as Red-footed boobies have a long reproductive period and the benefits to be gained from kinship selection may be expected to lead to more common trio formation.

Reversal in heterosexual mounting activity of ♂B over 2 years suggested potentially shared paternity; both males contributed to parental care because neither knew which was the father (Jamieson et al. 1994, DeLay et al. 1996). Paternal uncertainty could explain trio rarity among Red-footed Boobies, given the lack of benefit to male reproductive success of being a trio member. A future priority should be to conduct genetic analysis to ascertain chick parentage.

Cooperation may arise as a result of a skewed sex ratio (Young et al. 2008). We have no direct information on the sex ratio on Dong Island but, of ~ 2,000 nests inspected, only two cases of adult males breeding with females in immature plumage suggests the male:female ratio does not differ greatly from unity. We believe it is most likely that Red-footed Booby trio formation is an "opportunistic deviation" from the norm, as proposed for Common Terns (Ludwigs et al. 2004).

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Further Evidence of Breeding by Shiny Cowbirds in North America

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ABSTRACT.—We report evidence of egg-laying in northern Florida by the Shiny Cowbird (*Molothrus bonariensis*). Examination of the ovary and oviduct of a female trapped in Alachua County, Florida in late June 2006 revealed ovulation and recent passing of eggs. Two other Shiny Cowbird females captured in late May and early June had convoluted oviducts but showed no other signs of recent egg-laying. These three specimens add to the few female Shiny Cowbirds captured in North America. Our observations represent further evidence that Shiny Cowbirds likely breed in North America and additional evidence of breeding outside of southern Florida. *Received 10 August 2009. Accepted 10 December 2009.*

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The Shiny Cowbird (*Molothrus bonariensis*) is a generalist obligate brood-parasite that has been slowly expanding its breeding range northward over the last century from South America through the Caribbean to North America (Post et al. 1993, Cruz et al. 2000). Range expansion by the Shiny Cowbird has caused concern due to contact with novel hosts without recent exposure to brood

parasitism (Cruz et al. 1985). For example, arrival of Shiny Cowbirds in the West Indies threatened several endemic songbird populations (Wiley 1985, Cruz et al. 1989, Post et al. 1990). Shiny Cowbirds were first recorded in North America in southern Florida in 1985 (Smith and Sprunt 1987). By the mid 1990s, they were observed during the breeding season (Mar–Aug) in numerous localities (primarily coastal) throughout Florida (Cruz et al. 2000) and have been recorded in small numbers west along the Gulf Coast to Oklahoma and Texas, and north along the Atlantic Coast (Post et al. 1993) as far as New Brunswick, Canada (Benoit 1995).

Both male and female Shiny Cowbirds have been observed often in the southeastern United States (Post et al. 1993, Lowther and Post 1999), but the vast majority of specimens collected during the breeding season are males (ORNIS data base http://olla.berkeley.edu/ornisnet, accessed 6 July 2009). We report the collection of three female Shiny Cowbirds in Florida that contribute to only five other known females collected in North America (Sykes and Post 2001; W. Post, pers. comm.). Despite documented expansion of Shiny Cowbirds in the United States and a general increase in their abundance (Lowther and Post 1999), only a handful of records indicate breeding, most coming from southern Florida (Smith and Sprunt 1987, Kale 1989, Stevenson and Anderson 1994) and one from coastal Georgia (Sykes and Post 2001). We present further evidence of breeding by Shiny Cowbirds in North America through females collected in northcentral Florida.

METHODS

We captured birds in Alachua County, Florida (29° 39′ N, 82° 19′ W) from April to July 2006 and 2007 in drop-down traps (2.4 × 2.4 × 1.8 m) baited with food and live cowbird decoys as part of a study on reproduction of female Brown-headed Cowbirds (*Molothrus ater*). Traps were checked daily from 0900 to 1100 or 1400 to 1600 hrs EST. Trapping was conducted at cowbird feeding sites, including the University of Florida Beef Research, Horse Teaching, and Santa Fe Beef Research units.

Initial specimen identifications were performed at the Florida Museum of Natural History (Gainesville, FL) by AWK, using criteria in Pyle (1997). Specimens were prepared as round skins, and two tissue samples (muscle, liver, and heart) were saved from each. Few diagnostic features distinguish female Shiny from Brown-headed cowbirds, and genetic analyses of tissues were conducted at the Bell Museum of Natural History (St. Paul, MN) to confirm species identity. Whole genomic DNA was extracted from ethanol-preserved tissue samples using the QIAGEN Blood and Tissue Kit (Qiagen, Valencia, CA, USA). We amplified a 356-base pair region of the mitochondrial gene Cytochrome *b* and a 535-base pair intron from the Z-linked gene MUSK (muscle, skeletal, receptor tyrosine kinase) using a PCR protocol similar to Groth and Barrowclough (1999), but with an initial annealing temperature of 58° C. Primers used in PCR amplification and sequencing were L15656 (Barker 2004) and H16137 (Sorenson et al. 1999) for cyt b and MUSF-I3F, MUSF-I3R, and MUSK-I3F2 (Kimball et al. 2009) for MUSK intron 3. Successful amplification was confirmed on agarose gels and products were prepared for sequencing by enzymatic digestion (Werle et al. 1994). Sequencing was performed using BigDye Terminator technology on an ABI 3730 Sequencer and alignment was conducted by eye in the program SEQUENCHER (Genecodes, Ann Arbor, MI, USA). We compared the three unknown specimens to known *M. ater* and *M. bonariensis* sequences in Genbank (cyt b: AF089041, AF089043, and EF529951), and to new sequences obtained from vouchered tissue samples FMNH 334794 (cyt b: GU256541; MUSK: GU256545) and FMNH 350707 (MUSK: GU256546) to verify the identity of samples. Reference specimens of *M. ater* were collected in Illinois and Minnesota whereas those of *M. bonariensis* were from Puerto Rico.

Ovaries and oviducts were excised and weighed using a Mettler Toledo Analytical Balance (model AB54-S). Ovaries and oviducts were examined with a dissection probe and Bausch and Lomb Stereo Zoom 4 (7–30× magnification) dissecting microscope. Oviduct width was measured to the nearest millimeter using a standard metric ruler. Breeding condition of each female was assessed using pre-ovulatory and post-ovulatory follicles (Scott and Ankney 1983). Pre-ovulatory follicles represent developing ova that are subsequently released into the abdominal cavity and taken into the oviduct for egg production. Post-ovulatory follicles remain attached to the ovary after ovulation, and are reabsorbed over time. We recorded the number and size of any pre-ovulatory follicles (those that could potentially produce

TABLE 1. Reproductive measurements of female Shiny Cowbirds trapped in Alachua County, Florida, April–June 2007.

Specimen #	Collection date	Oviduct condition	Oviduct width (mm)	Oviduct mass (g)	Ovary mass (g)	Width of pre-ovulatory follicles (mm)	Area of post-ovulatory follicles (mm^2)
UF 45834	29 May	Minute, convoluted	2	<0.20	<0.05	None	None
UF 46076	8 Jun	Minute, convoluted	3	<0.20	<0.05	None	None
UF 46077	20 Jun	Enlarged, convoluted	8	0.9861	0.6055	9.41	6.17
						6.32	7.75 (atretic)
						3.56	

the yolk of an egg) in each specimen. Widths of pre-ovulatory follicles were measured to the nearest 0.01mm using a Mitutoyo Absolute Digimatic caliper (model CD6: CS). Round, orange-yellow pre-ovulatory follicles were distinguished from degenerating or atretic follicles which are irregular in shape and cream-colored. We also recorded the number and size of all recognizable post-ovulatory follicles, which are flat and oval-shaped and have an open slit (stigma) through which ova are released into the abdominal cavity during ovulation. Only follicles with ruptured stigma were considered post-ovulatory follicles and were distinguished from burst atretic follicles (Pearson and Rohwer 1998), which are ruptured but typically contain a cream-colored residue that is lacking in post-ovulatory follicles. The area of each flattened post-ovulatory follicle was estimated as the product of width and maximum lengths measured to the nearest 0.01mm.

RESULTS

Three (UF #'s 45834, 46076, 46077) of 147 female cowbird specimens collected were thought to be Shiny Cowbirds based on morphological characteristics, especially the longer, less deep bill, shorter wing, and longer tail of the Shiny versus Brown-headed cowbird (Pyle 1997). Comparison of known *M. ater* and *M. bonariensis* sequences revealed differences at nine sites at cyt b ($P = 0.03$ uncorrected distance) and three sites at MUSK ($P = 0.006$ uncorrected proportional distance). This difference in genetic distance among loci is expected as mitochondrial DNA is known to have a relatively rapid rate of evolution. All three unknown specimens had identical sequences at both the cyt b (Genbank Accession #'s GU256544, GU256542, GU256543) and MUSK (GU256549, GU256547, GU256548) loci. These sequences were a perfect match with *M. bonariensis* references at both loci. Our limited number of known references prevents us from addressing the extent to which these differences are polymorphic sites rather than fixed substitutions. The extent of differentiation and agreement of both mitochondrial and nuclear DNA provide compelling evidence in identifying the three specimens as *M. bonariensis*.

Two females collected (UF #'s 45834, 46076) showed no recent signs of egg-laying because they had small ovaries, minute oviducts, and no pre- or post-ovulatory follicles (Table 1). The oviduct of each of these females was convoluted indicating they had passed eggs during the current breeding season. The third female (UF # 46077) had numerous signs of recent egg-laying. The ovary had three orange-yellow pre-ovulatory follicles that were in good condition and followed a size sequence consistent with actively laying Brown-headed Cowbirds in Florida (MJR, unpubl. data). The size of the largest pre-ovulatory follicle was similar to follicles in Brown-headed Cowbirds that would likely have ovulated on the day following capture (MJR, unpubl. data). The ovary had one ruptured follicle that was likely post-ovulatory because the rupture occurred along the stigma and contained no residue that would be consistent with atresia. The size of this post-ovulatory follicle was similar to those in Brown-headed Cowbird daily laying sequences that were estimated to have ovulated 4 days before collection (MJR, unpubl. data). The ovary also included one atretic follicle that was flaccid, lacked a clearly ruptured stigma, and contained cream-colored fluid. The oviduct of the specimen was large (~ 1g) and convoluted indicating it passed an egg during the current breeding season. Mass measurements of the ovaries (range = 0.1224–0.9172 g, $\bar{x} = 0.4335$ g, SD = 0.1853 g) and oviducts (range = 0.5802–1.8511 g, $\bar{x} = 1.2569$ g, SD = 0.2902 g) of 46 female Brown-headed Cowbirds in breeding condition (MJR, unpubl. data) were similar to those for this specimen.

Collection dates for all three specimens were within the period when the majority of female Brown-headed Cowbirds in Florida are in breeding condition (26 Apr–24 Jun) (MJR, unpubl. data).

DISCUSSION

Shiny Cowbirds have been reported in the United States, especially Florida, during the breeding season for nearly 25 years. To date, however, there has been scant evidence of breeding. Seven of eight male Shiny Cowbirds captured in the southeastern U.S. in 1992 had enlarged testes (Post et al. 1993), and male cowbirds have been observed courting females (Post et al. 1993, FFWCC 2003). However, it is not clear in these cases whether copulation and subsequent egg-laying occurred. There are four observations of fledgling Shiny Cowbirds from southern Florida, three of which were being fed by adults of other species (Smith and Sprunt 1987, Kale 1989, Stevenson and Anderson 1994). These records are not considered definitive (Lowther and Post 1999) because of difficulties distinguishing between juvenile Shiny and Brown-headed cowbirds. The latter species has also recently expanded into the southeastern U.S., occurs in much higher numbers, and has been confirmed breeding throughout Florida (FFWCC 2003). However, Sykes and Post (2001) captured a female Shiny Cowbird on the coast of Georgia in early July 2000 that had an enlarged ovary and three developing ova in its oviduct. Until now, no further substantial evidence of breeding by Shiny Cowbirds in North America has been reported.

We note our records also cannot be considered definitive. The two females with convoluted oviducts may have passed eggs earlier in the breeding season, but no other signs of recent reproduction were evident. Shiny Cowbirds may be capable of substantial long-range movements (Post et al. 1993), and breeding could have occurred outside of North America. It is also possible the female that was in reproductive condition may have ovulated and laid unfertilized eggs. However, the appearance of the ovary and oviduct indicate the female would have produced a series of unfertilized eggs. We regard this as unlikely. Furthermore, we do not know if eggs produced by this female were laid in an appropriate location (i.e., a potential host nest). Our observation of a female Shiny Cowbird in reproductive condition that likely recently passed an egg lends support to breeding by Shiny Cowbirds in the United States.

The initial colonization of Florida and the southeastern United States by Shiny Cowbirds provoked alarm about negative impacts on native breeding species (Atherton and Atherton 1988, Paul 1988). Extremely limited documentation of breeding by Shiny Cowbirds and near absence of collected females after nearly 25 years in the southeastern United States indicate that either the species is having little success colonizing mainland North America, or that difficulties in documenting breeding and/or identifying females or juveniles resulted in underreporting of breeding by this species. Focused collection studies of cowbirds may be helpful in identifying the extent of breeding by Shiny Cowbirds in these initial decades of colonization of mainland North America. Collections will likely improve Shiny Cowbird abundance estimates by avoiding difficulties in differentiating females of similar cowbird species.

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Circumstantial Evidence for Infanticide of Chicks of the Communal Smooth-billed Ani (*Crotophaga ani*)

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ABSTRACT.—The Smooth-billed Ani (*Crotophaga ani*) is a plural-breeding, joint-nesting species that engages in both cooperation and reproductive competition. We report circumstantial evidence for infanticide of chicks by adults that joined a group after completion of the communal clutch. We provide evidence that some of the group adults captured after the infanticide were unrelated to any of the chicks and may have acted to increase chances of renesting. *Received 30 July 2009. Accepted 3 December 2009.*

Infanticide of young by adults is an infrequent, yet widespread behavior among many taxa

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(Bertram 1975, Hrdy 1979, Sherman 1981, Hrdy and Hausfater 1984) and, in some species, it represents a considerable proportion of juvenile mortality (Sherman 1981, Packer and Pusey 1983). It is typically considered a reproductive strategy associated with reducing wasted resources or parental care directed towards unrelated young by potential foster parents (Pierroti 1991, Quinn et al. 1994, Eggert and Müller 2000) or step-parents (Rohwer et al. 1999).

Resources and care in cooperatively breeding species are often directed towards non-filial young. A number of features, including genetic relatedness among adult group members within cooperatively breeding groups, affects which individuals breed and how much. Infanticide has been proposed as a mechanism to adjust a group's reproductive skew, the extent to which individuals monopolize reproduction (Clutton-brock et al. 1998, Hager and Johnstone 2004, Macedo et al. 2005). Reproductive skew may be adjusted to support group stability (Vehrencamp 1977, 1978; Vehrencamp and Quinn 2004), but immigrants arriving soon after fertilization are likely to be compromised by delayed reproduction if offspring care is costly.

Power struggles and resultant take-overs have been described in social animals including lions (*Panthera leo*) (Bertram 1975, Packer and Pusey 1983) and Acorn Woodpeckers (*Melanerpes formicivorus*) (Koenig 1981, Hannon et al. 1985). The immigrant individual or group, in these cases, displaces existing same sex group members and subsequently may kill existing offspring. Infanticide has been reported in communal breeding animals, although the evidence is often indirect as observing infanticide directly is unlikely (Stacey and Edwards 1983). Research to establish the relatedness of victims and perpetrators is needed, particularly in plural-breeding species, species with breeding groups in which more than one male and female are breeders (Trail et al. 1981, Macedo et al. 2001).

The Smooth-billed Ani (*Crotophaga ani*) is a plural-breeding, joint-nesting neotropical cuckoo of the subfamily Crotophaginae. Anis form socially monogamous pairs that cooperate as a communal group to raise mixed broods of young in a single nest (Davis 1940, Quinn and Startek-Foote 2000). Ani group size ranges from two to 17 individuals with up to five females, typically unrelated to each other (Quinn and Startek-Foote 2000; J. S. Quinn, unpubl. data). Genetic data confirm that extra-pair fertilizations occur in this species (J. S. Quinn, unpubl. data). Smooth-billed Anis engage commonly in egg tossing and egg burial, resulting in failure of an average of 56% of eggs laid by multi-female groups (Schmaltz et al. 2008). These behaviors may lead to reduced competition for young hatching from eggs that are typically laid after tossing or burial episodes by their parents. Skewing reproduction may explain this behavior, but it is possible that ovicidal adults are increasing hatching synchrony to limit size asymmetry that might lead to death of their young. Our objectives are to: (1) describe circumstantial evidence for chick infanticide, and (2) show that some adults in the group after the apparent infanticide were unrelated to the nestlings and may have been new group members.

METHODS

Adults in groups were counted once a month as they departed roosts during the morning and numbers were recorded opportunistically during nest checks. Nests were checked daily during laying until incubation began and then were resumed 2 days prior to expected first hatching. Adults were captured using mist nets and playback in early morning at the roost site. Blood samples were taken from captured adults and chicks to allow microsatellite genotyping and parentage exclusion. We genotyped with six microsatellite loci (450B2, C5, C14, SNX07, SNX14, and SNX17; Blanchard and Quinn 2001, Gregory and Quinn 2005). Relatedness (Queller and Goodnight 1989) was examined using GenAlEx6.2 (Peakall and Smouse 2006).

OBSERVATIONS

We observed dead chicks or their disappearance in 23 of 90 broods monitored over 10 years of study, generally September through December or early January inclusive from 1998 until 2007 at Cabo Rojo National Wildlife Refuge, Puerto Rico (17° 59′ N, 67° 10′ W). We inferred the loss of 10 broods (43.5%) to have been caused by brown rats (*Rattus rattus*), Red-tailed Hawks (*Buteo jamaicensis*), or red fire ants (*Solenopsis invicta*) based on direct observations or signs at the nest (Table 1). The collected evidence from one case does not appear to be the result of these predators and is more consistent with infanticide. We observed chicks that had been recently killed with skin stripped off the skull in 2006 in the

TABLE 1. Numbers of failed Smooth-billed Ani broods monitored between 1998 and 2007 (inclusive) and likely cause with evidence.

Number of broods	Suspected cause	Evidence/sign of predation at nest
4	Red-tailed Hawk	Small bits of flesh left in the nest; eggs were not predated; one observed on time lapse videotape.
2	Rat	Bone fragments remained in nest; small sharp tooth indentations in plastic color bands in one case; only body left (head eaten) in other case. Video observations indicate that rats completely eat newly hatched nestlings starting with the head.
4	Red fire ant	Small pustules on skin of dead chicks; ants seen on chicks or in nest.
12	Unknown	Chicks too young to leave nest; nothing remaining. Most consistent with rat or Red-tailed Hawk predation.
1	Infanticide	Scalp split, skull showing; aggressive vocalizations and movement of adults near nest; post-laying period increase in group size.

"Gully" group and describe known circumstances along with microsatellite genotype data for some captured adults and the nestlings (Table 2).

A small group of up to four adults (2 banded and 2 not banded) occupied the territory, bred, and tended eggs in a nest discovered by us after clutch completion. Genetic analysis suggested the presence of an additional breeding male and female (likely unbanded and hence less detectable, or brood parasitism by a non-member of the group). A color-banded bird that had not previously been observed on territory was seen shortly after the last young hatched and observations showed that at least four additional adults had recently joined the group. We observed at least seven adults in the nest tree on 18 October engaging in aggressive vocalizations and interactions that were obscured by foliage. We observed no chick-predators in the area during this time. We found two dead chicks in the bottom of the nest following these observations. Four living nestlings observed on 18 October were not seen again and are presumed to have died. We subsequently captured three adults beside the nest tree using mist nets and playback. One month after the nestling deaths we observed one of the adults, which had been banded on 22 October, nest building on another territory (Table 2).

We genotyped all six Gully-group nestlings and all identified color banded adults. Dyads of

TABLE 2. Timing of events in 2006 at the Smooth-billed Ani nest on the "Gully" territory.

Date	Observations
16–28 September	Up to 4 birds including color-banded RG/A (male), WY/YAblt (female), and unbanded birds observed in territory.
28–29 September	Two birds carrying nesting material.
2 October	Nest found with 6 eggs (many tossed eggs beneath).
12 October	Eggs 1, 2, and 3 hatched.
14 October	Six chicks – 3 new from eggs 4, 5, and 6.
15 October	GWYAb (first and only time observed in territory)[a].
16 October	Four adults observed at nest; 1 with food.
18 October	Six or 7 adults in nest tree; aggressive vocalizations heard several times; copulation observed between unbanded male and female with Ag on right leg; 2 dead nestlings in nest; 1 chick scrambled away; 3 chicks banded.
21 October	Seven adults observed at nest tree; no further record of live chicks on territory.
22 October	Three adults captured and banded: BB/AbY (female), RG/AbR (female), WR/AbW (male).
5 November	Up to 10 adults observed together on territory interacting without aggression: 6 unbanded, 3 or 4 banded including: BB/AbY (female), RG/AbR (female), and WY/YAblt (female).
16 November	BB/AbY (female) and unbanded bird observed nest building in another territory east northeast at least two territories distant (~ 1 km).
16 December	RG/AbR (female) and WR/AbW (observed in "Gully" territory).

[a] Band combination misread.

TABLE 3. Exclusion analysis of sampled adults and young from the 2006 "Gully" territory based on six ani microsatellites. "Included" individuals are those with genotypes consistent with parentage of particular chicks. "Included" pairs have genotypes consistent with parentage by the included pair. "Excluded" adults are not shown.

Chick	Included females	Included males	Included pairs
A	WY/YAblt, RG/AbR	RG/A	RG/A × WY/YAblt
B	WY/YAblt		
C	RG/AbR		
D	RG/AbR	RG/A	RG/A × RG/AbR
E		RG/A, RW/AbW	
F	RG/AbR		

sampled adults in the group showed mean (± SE) relatedness values of −0.083 ± 0.105 (range −0.28 to +0.30). These values suggest the adults sampled were not close relatives, consistent with analyses of other Smooth-billed Ani groups (J. S. Quinn, unpubl. data). Exclusion analysis suggested the two previously color banded adults associated with the territory during egg laying were parents of some young as was one of the adults captured subsequently (Table 3).

Observations (Table 2) and genotyping (Table 3) are consistent with an immigration event and subsequent infanticide as group size increased after clutch completion. Some group members were not related to any of the young, providing a likely motive for infanticide (to reduce the time to the next breeding attempt; Macedo and Melo 1999). Aggressive behavior occurred in the nest tree on the day the two dead offspring were discovered. We did not see the remaining four offspring subsequently and presumed they had died. Banded individuals that had been seen on the territory prior to clutch completion and one that was caught subsequently were likely genetic parents of some of the young. The remaining individuals captured after clutch completion were not closely related to any young or sampled adults in the group.

Elimination of offspring at the chick stage is not the only way to initiate renesting. We have tracked egg rejection for several years. Most of those cases were limited to the egg-laying phase and did not lead to renesting, but we observed two cases, both in 2003, where eggs were apparently pecked, leaving a large hole in each. Thirty eggs were laid, three of those were ejected from the nest, nine were buried in the nest structure, and 18 eggs were pecked leading to nest abandonment in one group of 12 birds ("North House"). Thirty eggs were laid by another group of seven adults ("South Fence"); two of those were ejected, 26 were buried in the nest structure, and the remaining two in the nest bowl were pecked leading to nest abandonment. Both of these groups were multi-female breeder groups. We have not observed other avian species that are egg predators near nests of Smooth-billed Anis and suspect these cases were egg rejection. The abandonment presumably increased chances for renesting. The North House group did renest successfully soon after the clutch destruction. Eggs were destroyed between 19 and 22 November 2003 and the new nest was found on 8 December with 15 eggs in the nest cup, two tossed eggs beneath, and five buried eggs. Twenty-two eggs were laid over a maximum of 16 to 19 days; therefore, the new nest was initiated soon after the eggs in the previous nest had been destroyed.

DISCUSSION

Egg rejection is a reproductive tactic that we previously described as common in Smooth-billed Ani groups (Schmaltz et al. 2008). Egg rejection is limited to groups with more than one breeding female and may relate to reproductive competition (Schmaltz et al. 2008). Destruction of complete clutches led to nest desertion and subsequent renesting in one of the two cases described here. Macedo et al. (2005) argue that individuals failing to lay or fertilize eggs in the group nest may engage in infanticide (or ovicide) to initiate a renesting in which they may improve their reproductive success. The ovicide described here is consistent with either intra-group activity or with a joining event following clutch completion.

Infanticide of Smooth-billed Ani chicks has not been directly observed, but we report indirect supporting evidence. Alternative hypotheses are possible, but our circumstantial evidence suggests the chicks were killed by new group members, unrelated to the offspring, presumably to hasten a new reproductive bout (Macedo and Melo 1999).

These observations are consistent with other competitive behaviors seen in this communal nesting species.

Our observations on infanticide support group joining over a territory take-over by a rival group. Habitat did not appear to be in shortage. We have observed vacant territories that are used some years and not others during ongoing research suggesting that Smooth-billed Ani habitat was not saturated in our study area (J. S. Quinn, unpubl. data). Observed aggression associated with other territory intrusion events included apparent trespassing by neighbors, or group joining events by one to several individuals (J. S. Quinn, unpubl. data). We have not observed a territory take-over. The group membership following the "immigration event" reported here included both original members and new birds. Subsequent observations did not include within group aggression, although one of the presumed immigrants was later seen nest building on another territory suggesting the group was not completely stable following the immigration.

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Flight Speeds of Migrating Red-necked and Horned Grebes

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ABSTRACT.—Air speed of Red-necked Grebes (*Podiceps grisegena*), migrating in "no wind" conditions along a 2.64-km path along Lake Superior, Michigan in fall averaged 61.5 km/hr. Speed increased significantly using tail winds adjusted for wind vectors as the migration season advanced: 68 km/hr in August, 70.1 km/hr in September, and 78.7 km/hr in October. Horned Grebes (*P. auritus*) averaged 55.5 km/hr with no winds and, with tail winds, increased from 63.5 km/hr in September to 71.5 km/hr in October. Whether the increases indicate that late fall migrants are time constrained to complete their movement to wintering areas rapidly, or are a consequence of having to fly faster because of larger body mass at that season, remain to be fully explored. We also present flight speeds of 10 additional species of waterbirds migrating along the same path. *Received 22 April 2008. Accepted 28 October 2009.*

The north shore of Keweenaw County, Michigan, at the tip of the Keweenaw Peninsula, is a leading line for waterbirds migrating from west to east over Lake Superior (Binford 2006). Fall migrants fly due east, close to and parallel to the shoreline, and rarely vary their altitude, direction, or speed making this an ideal location for studying flight speed. Red-necked Grebes (*Podiceps grisegena*) and Horned Grebes (*P. auritus*) are among the common migrants. We took advantage of the exceptional observation conditions to measure their flight speed under differing conditions at several phases of the fall migration. We also documented speeds for other passage waterbirds.

METHODS

Study Area and Field Methods.—The south shore of Lake Superior in Keeweenaw County, Michigan trends west-east. We selected two locations, "Dan's Point," 6.4 km west of Copper Harbor, and "Kirkish Point," 3.8 km west of town for observations. These peninsulas project farther into the lake than others in Keweenaw County. We chose a spot at each locality within sight of the other, about 5 m above lake surface, and on a west-east line paralleling the coast. Surveyor R. S. Haataja measured the distance at 2640.35 m using Ashtech GPS (Global Positioning System) receivers and double-checking the data with a Topcon GPT 1003 Total Station using infrared beam and reflector. We used 2,640 m in our calculations. I. D. Wijayratne located a spot on the bedrock 14 m due north of each point and about 5 m above lake level using an optical transit. We marked these with orange paint and positioned over each an orange pole 4 cm in diameter and 3 m tall. We directed a 20× spotting scope at the pole at each point. We timed birds using identical, continuously running stop watches, synchronized at the start of each session, and used citizen-band radios to communicate between stations.

We gathered data on mornings between 13 August and 21 October 1999–2003. Binford manned the west point, and Youngman (replaced by Jake Musser in 2003) was at the east point. We used binoculars to detect grebe migrants and

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[3] Deceased.

switched to spotting scopes for counting and timing. Binford chose which individuals or flocks to time, spacing his choices to give Youngman sufficient time to complete the previous observation. Binford detected subjects arriving from the west. When the lead bird's head was aligned with his pole, he used a stopwatch to record the time to the nearest second. He then radioed Youngman and gave him an unique observation number, total flock size, and the identity of included species, including the lead bird, and the approximate distance offshore ("close," "moderate," or "far"). Youngman used the last datum to locate flocks, which he was usually able to detect quickly, giving ample time for verification and recording time of passage, along with wind and temperature data. Each member of a flock was considered to have the same time as the lead bird if the distance between the leader and the following birds remained the same (data from shifting flocks were eliminated).

Youngman used an anemometer (Skywatch Meteos, JDC Electronics, Yverdon-les-Bains, Switzerland) to measure wind velocity and direction. He recorded high and low wind speeds during a 15-sec period immediately after a flock passed his pole and used the means to calculate air speed. Winds <3 km/hr, or too variable to ascertain direction, were considered 0 speed. Only observations with west or north-northwest, or east to east-northeast winds were used. Flight speeds with southerly components were excluded because the land mass sheltered the anemometer, although not birds over the lake.

We minimized problems inherent in timing birds over a measured course (Schnell 1965). Clicking a stopwatch at exactly the same instant a bird reached a pole was difficult. However, both observers had the same problem and responded at about the same time in relation to bird-pole position, the distance actually measured was nearly the same as pole to pole. We doubt this difference exceeded 1 sec, which is negligible considering the time (2+ min) for most birds to complete the course. Most recorded birds flew <30 m above the water, sufficiently low that wind speeds probably differed little from those at shore observation points.

We ignored birds flying westward (possibly slowing to search for foraging areas) and excluded flocks in which birds changed direction, shifted internal position, merged with another flock, or obviously changed speed. We deleted the observations if there were discrepancies between the two sightings (e.g., number of birds, identity of lead bird, distance offshore).

Statistical Analysis.—We calculated air speed as recorded ground speed minus vectored tail wind (W, NW) velocity or plus vectored head wind (E, ENE) velocity. Vectoring assumed that due west and east winds were 100% effective, east-northeast 75%, and northwest 50%. We used one-way analysis of variance (ANOVA, Minitab Version 13 for Windows) to test for significance of difference in air speed between months, and between tail, head, and zero winds.

RESULTS

All 70 Red-necked Grebe flocks for which we obtained useful data were migrating in W (n = 25,) NW (n = 26), ENE (n = 6), E (n = 6), or zero (n = 7) winds. Thirteen were of single individuals. 32 contained 2–14 individuals, and 6 contained 17–35 birds; 13 flocks were mixed with other species. There was no significant difference in flight speed among these groups. Flight speeds averaged ~ 60 km/hr in "no wind" conditions throughout the fall migration, but tail wind speeds were progressively greater as the season advanced (Table 1): August—61.8 km/hr; September—70.0 km/hr; October—78.7 km/hr. The differences were statistically significant (F = 41.89; df = 2; P = 0.001). Air speeds were unrelated to wind conditions, at least in August and September, as indicated by similar tail wind velocities in August (10.8 km/hr) and September (10.7 km/hr).

All 17 Horned Grebe flocks were moving in NW (n =14), E (n =1), or zero (n = 2) winds. Twelve contained 3–8 individuals, and one contained 14; four flocks consisted of mixed species, total individuals ranging from two to nine. This species, perhaps because of its slow speed and unique behavior of flying low, at times below wave crests, rarely joined other species, and did not lead a mixed-species flock; no other species joined a flock composed predominately of Horned Grebes. "No wind" speed averaged 55.5 km/hr in October. Tail wind speed increased from 63.5 km/hr in September to 71.5 km/hr in October (F = 21.14; df = 1, P = 0.001), even though similar wind speeds prevailed in both months (9.3 km/hr and 9.0 km/hr, respectively).

Data for other species of waterbirds were obtained during the same periods (Table 1).

TABLE 1. Flight speeds (km/hr) of waterbirds migrating eastward over Lake Superior off Keweenaw County, Michigan, in fall.

Species	Tail wind Mean ± SD Range (*n*)			Head wind Mean ± SD Range (*n*)			No wind Mean ± SD Range (*n*)	
	Ground speed	Wind speed (vectored)	Air speed	Ground speed	Wind speed (vectored)	Air speed	Wind speed	Ground and air speed
Red-necked Grebe	80.4 ± 10.5 64.5–105.6 (51)	11.8 ± 3.2 6.8–29.8 (51)	68.7 ± 8.4 54.2 ± 85.6 (51)	54.8 ± 2.8 50.4–59.1 (12)	5.3 ± 2.2 1.0–7.6 (12)	60.1 ± 3.5 53.8–66.1 (12)	0 (7)	61.2 ± 2.5 58.7–66.5 (7)
13–23 Aug	72.6 ± 4.2 64.5–81.9 (21)	10.8 ± 2.5 7.2–15.8 (21)	61.8 ± 3.9 54.2–69.0 (21)	55.1 ± 3.0 50.4–59.1 (9)	6.3 ± 0.8 5.6–7.6 (9)	61.4 ± 2.9 57.3–66.1 (9)		
9–17 Sep	80.7 ± 8.4 6.0–95.1 (18)	10.7 ± 2.7 6.8–13.9 (18)	70.1 ± 6.4 59.1–82.1 (18)	54.0 ± 2.3 52.5–56.7 (3)	2.3 ± 2.2 1.0–4.8 (3)	56.2 ± 2.1 53.8–57.6 (3)		59.9 (1)
2–14 Oct	93.6 ± 7.6 82.7–105.6 (12)	14.9 ± 8.0 8.1–29.8 (12)	78.7 ± 5.0 72.4–85.6 (12)					61.5 ± 2.7 58.7–66.5 (6)
Horned Grebe	76.1 ± 5.6 66.9–83.4 (14)	9.2 ± 2.2 6.8–16.1 (14)	66.9 ± 5.2 58.6–73.9 (14)	54.1 (1)	8.2 (1)	62.3 (1)	0 (2)	55.5 53.8–57.3 (2)
12–17 Sep	72.7 ± 4.7 67.0–81.3 (8)	9.3 ± 2.9 6.8–16.1 (8)	63.5 ± 3.9 58.6–70.5 (8)					
10 Oct	80.5 ± 2.7 76.1–83.4 (6)	9.0 ± 0.8 7.7–10.1 (6)	71.5 ± 2.1 68.4–73.9 (6)	54.1 (1)	8.2 (1)	62.3 (1)	0 (2)	55.5 53.8 –57.3 (2)
Common Loon *Gavia immer*	86.9 80.6–93.2 (2)	16.2 6.0–26.4 (2)	70.7 66.8–74.7 (2)	65.7 65.5–66.0 (2)	4.3 2.3–6.4 (2)	70.1 68.2–71.9 (2)	0 (10)	70.2 ± 5.6 61.8–76.1 (10)
American Wigeon *Anas americana*	79.3 70.5–88.0 (2)	10.2 8.0–12.3 (2)	69.1 62.4–75.8 (2)				0 (1)	68.4 (1)
Green-winged Teal *A. crecca*	76.7 ± 4.3 70.5–79.8 (4)	8.6 ± 2.5 6.8–12.2 (4)	68.1 ± 4.4 62.4–72.4 (4)					
Greater Scaup *Aythya marila*	76.6 (1)	8.5 (1)	68.1 (1)	52.5 (1)	4.8 (1)	57.3 (1)	0 (2)	64.9 58.7–71.0 (2)
Surf Scoter *Melanitta perspicillata*				56.9 52.8-61.0 (2)	11.3 10.8–11.9 (2)	68.2 63.6–72.9 (2)		
White-winged Scoter *M. fusca*	89.8 ± 9.0 76.6–104.4 (6)	11.4 ± 4.5 7.6–20.0 (6)	78.5 ± 3.5 68.0–84.5 (6)	56.9 ± 6.8 47.0–66.5 (6)	8.5 ± 4.1 1.9–12.4 (6)	65.4 ± 6.3 59.4–76.4 (6)	0 (1)	58.7 (1)

TABLE 1. Continued.

Species	Tail wind Mean ± SD Range (*n*)			Head wind Mean ± SD Range (*n*)			No wind Mean ± SD Range (*n*)	
	Ground speed	Wind speed (vectored)	Air speed	Ground speed	Wind speed (vectored)	Air speed	Wind speed	Ground and air speed
Black Scoter				47.0	12.4	59.4		
M. nigra				(1)	(1)	(1)		
Long-tailed Duck				47.0	12.4	59.4		
Clangula hyemalis				(1)	(1)	(1)		
Common Goldeneye				57.9	10.3	68.2		
Bucephala clangula				(1)	(1)	(1)		
Red-breasted Merganser	86.7 ± 6.4	9.6 ± 1.2	77.2 ± 7.1	58.5 ± 5.6	8.3 ± 1.9	66.8 ± 1.3		
Mergus serrator	82.7–94.1 (3)	8.9–10.9 (3)	72.4–85.3 (3)	57.9–59.1 (2)	6.9–9.7 (2)	66.0–67.6 (2)		

DISCUSSION

Measured flight speeds for grebes are almost non-existent, and no data for either the Red-necked or Horned grebe are presented in recent *Birds of North America* compilations (Stout and Nuechterlein 1999, Stedman 2000). We found flight speeds in windless conditions averaged 61.2 km/hr for Red-necked Grebes and 55.5 km/hr for Horned Grebes (vs. 60 km/hr for Eared Grebes [*P. nigricollis*]; Cullen et al. 1999).

Air speeds for both species increased through the fall migration period, even when tail winds were considered. This increase may have relevance to the question of whether migrants fly at minimum power velocity (V_{mp}), maximum distance velocity (V_{md}), or somewhere in between (e.g., Alerstam 1990, 2003). Tail wind data, for example, suggest that Red-necked Grebes fly slower in August, just as they are arriving at the Great Lakes (where many stop and molt), and that speeds increase progressively in September and October, as the grebes prepare to leave for wintering areas on the Atlantic Coast. The Horned Grebe had a similar pattern for September–October. This pattern might indicate that grebes in early fall emphasize energy conservation, whereas in late fall migration, when time to reach wintering areas is constrained, the ability to fly faster and cover long distances rapidly is more important. However, larger birds necessarily fly faster than smaller birds of the same species, because flight speed is proportional to mass $^{1/6}$ (Rayner 1988). Data on weight changes in migrating Red-necked and Horned grebes are not available. Eared Grebes lay on large fat stores while at fall staging areas, so that body mass is 50% greater on departure than on arrival (Jehl 1988, 1997; Jehl et al. 2003; Jehl and Henry 2010). If Red-necked and Horned grebes show a similar pattern, the expected increase in air speed between arriving and departing birds would approximate 5%, which is much less than we found in early versus late fall samples. Additional data on mass and body composition of these species at different seasons are needed to move the discussion forward.

Regardless of whether the increased speed is due to behavioral adjustment, increased body mass, or both, seasonal differences in flight speed can be expected. Detailed interspecific or intra-

specific comparisons must use data from the same time period or from birds in the same physiological condition. For this reason, the data in Table 1 should be used cautiously.

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Thermoregulatory Behavior in Migratory European Bee-eaters (*Merops apiaster*)

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ABSTRACT.—Birds in hyper-arid environments have acute problems of energy and water balance, and thermoregulate both physiologically and behaviorally. I report on European Bee-eaters (*Merops apiaster*) engaged in a previously unreported thermoregulatory behavior of diving into the sea and in salt ponds with high levels of salinity. This behavior may also explain the previously reported, but unexplained, finding of bee-eaters inside a tiger shark (*Galeocerdo cuvier*) in the Red Sea. These observations should instigate future experiments on the subject of selective use of salt water for evaporative cooling and thermoregulatory behavior by desert birds. *Received 27 August 2009. Accepted 9 December 2009.*

Animals in deserts use a variety of mechanisms to maintain their body temperature within physiologically acceptable limits and minimize water loss (Louw and Seely 1982). Heat stressed birds engage in panting or gular fluttering to affect evaporative cooling (Tieleman 2002, pers. obs.). Other physiological adaptations in hot environments include greater tolerance of tissues to high temperatures and dehydration, heterothermy (fluctuation of body temperature in response to environmental stress), reducing insulation, and appropriate coloration (Louw and Seely 1982, Maclean 1996, Tieleman 2002).

Behavioral thermoregulation is a suite of behavioral activities that minimize the exposure of the organism to heat stress and reduce water loss at high temperatures (Wunder 1979). It is

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common to see birds exploit cooler terrestrial micro-climates and bathe in water to remove body heat by evaporative cooling (Dawson and Bartholomew 1968, Cook 1997).

The International Birding and Research Centre in Eilat, Israel has reclaimed a local garbage dump as a Bird Sanctuary to help migratory bird populations (Cherrington 2001, Tal 2002, Rosenzweig 2003). The site has commercial salt ponds and a fresh water lake that are less than 50 m apart. Eilat is at the southernmost tip of Israel within the Sahara-Arabian desert belt characterized by extreme temperatures (mean = 9.5 to 39.4° C; Israel Meteorological Service, www.ims.gov.il), very low precipitation (mean annual rainfall = 17 mm), and high solar radiation (mean = 6.32 kWh m^2/day, Faiman et al. 2003).

I report observations of migrant European Bee-eaters (*Merops apiaster*) diving into the sea and salt ponds with high levels of salinity (>15%).

OBSERVATIONS

European Bee-eaters migrate through the Eilat bottleneck in both seasons in large numbers. They are among the last migrants in spring (May–Jun) and their passage at Eilat coincides with the peak heat waves of late spring–early summer when ambient temperatures can range from 18 to 48° C. Temperatures peak on many occasions during periods of khamsins, dry, hot, and dusty local wind that carries great quantities of sand and dust from the deserts with speeds to 160 km/hr, and a rise of temperatures as much as 20° C in 2 hrs.

I observed 57 flocks of bee-eaters diving into the shallow salt ponds in the Bird Sanctuary or off-shore in the Red Sea in spring 2005–2009 for a total of 36 khamsin days with temperatures above 43° C. Similar observations were also made from the shores of the Red Sea. However, the outcome of this behavior far out at sea was too distant to describe properly. Bee-eaters were also present on days when temperatures were under 42° C, but were not observed diving into the salt ponds. All observations were conducted with Swarovski 15 × 56 binoculars.

Bee-eaters perched in the shade of *Prosopis alba* and *Acacia raddiana* trees surrounding the salt pond at the southern extremities of the Bird Sanctuary. I considered them heat stressed because of their open beaks, tongues thrust out and gular fluttering. Every 15–20 min small groups of bee-eaters, 8–39 birds/flock, would take off and dive head first into the shallow salt pond. On most occasions the whole flock would take off in a circling flight, calling, and diving into the salt pond. Rarely did single birds remain behind when the flock was engaged in diving.

The bee-eaters flew into the shadiest parts of the trees and perched there for the next 30–45 min after flying from the water, or paddling to the shoreline. The bee-eaters spread their wings while wet and allowed the breeze and the low humidity of the area (15–18%) to dry the feathers during the period immediately after they perched. I believe the birds achieved evaporative cooling since bee-eaters did not engage in gular fluttering for the first 15–20 min after diving.

The maximum depth of the salt pond was 200 mm. I observed 576 bee-eaters diving into the ponds with 389 flying from the water surface and 111 unable to do so and had to paddle ashore where they lay on the ground for several minutes with their wings stretched out before flying to a perch. The remaining 76 bee-eaters were dazed for many minutes, possibly from hitting the bottom of the pool. They surfaced from the dive but did not move, and had trouble reaching the shoreline. These birds were collected, rehabilitated (allowed to rest in the shade and fed sugar water), and returned to the wild a day or two later. On days when I was not present at the Bird Sanctuary, 117 carcasses washed up on shore suggesting this is a common phenomenon.

I saw no bee-eaters diving into the nearby fresh water lake which is much deeper (~ 4 m), and which has fish.

DISCUSSION

Fry (1984, 2001) reviewed bathing (a.k.a. splashing) by several species of bee-eaters. The major reasoning forwarded by most published reports was that bee-eaters were feeding on insects or fish. Fry (2001:313) states that cooling, dislodging parasites, drinking or cleansing are alternatives to what seems "to be essentially some sort of social comfort activity" in the gregarious bee-eaters. My observations of bee-eaters diving into salt ponds, devoid of fish or other possible food sources, during the hottest days of the season strengthens the argument that in the desert "splashing" has a thermoregulatory function.

The described behavior may explain the finding of bee-eaters inside a tiger shark (*Galeocerdo cuvier*) in the Red Sea (Yosef et al. 2002). Perhaps the Bee-eaters involved had dived into the Red Sea for cooling and were unable to take off from

the surface and were eaten by the shark, or had drowned and collected from the body of water. The latter appears to be the more realistic option because tiger sharks are considered to be nocturnal foragers (Compagno and Niem 1998).

The ability of some birds to discriminate fresh and saline waters is debated (Maclean 1996). However, most studies have investigated the tolerance of birds to saline water – drinking tolerance, body mass loss, serum and urine osmolarity, and fecal water loss (Maclean 1996). It has also been suggested that a possible added value could be the removal of ectoparasites in the salt water. However, this has yet to be proved. I was unable to find literature on how birds use water sources and modify their behavior to thermoregulate in extreme temperatures. King and Chastant (2008) report on cormorants (*Phalacrocorax* spp.) and darters (*Anhinga* spp.) that regurgitate water into their chicks open mouths and over their bodies on warm and windless days during the hottest hours to help them maintain their body temperatures.

We still lack information on the ability of seawater to have a cooling effect on heat-stressed birds. My observations should instigate future experiments on the subject of evaporative water loss and thermoregulatory behavior in desert birds.

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Population Status of Chuck-will's-widow (*Caprimulgus carolinensis*) in the Bahamas

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ABSTRACT.—The Chuck-will's-widow (*Caprimulgus carolinensis*) in the Bahama Islands has been regarded as a rare to uncommon winter visitor. We conducted breeding season surveys on the three largest northern islands (North Andros, Grand Bahama, and Great Abaco) to examine the status of this species. We encountered singing birds on most survey routes on all three islands, suggesting that sizeable breeding populations are widespread in the northern Bahamas with an aggregate estimate of 500–1,000 pairs. Our density estimates were somewhat less than those from the primary range in the United States, suggesting either a lower carrying capacity in the Bahama Islands or recently established populations that have yet to reach carrying capacity. *Received 24 August 2009. Accepted 3 January 2010.*

Much remains to be learned about Chuck-will's-widow (*Caprimulgus carolinensis*) and other nightjars (Caprimulgiformes), largely because of their nocturnal and secretive habits. The species breeds across much of the eastern United States and winters in southern Florida, Central America, the West Indies, and northern South America. Gaps remain in our knowledge of the species' distribution, abundance, and habitat use despite its distinctive nocturnal song, which greatly facilitates detection (Straight and Cooper 2000). The species has gradually expanded its range in North America in the past century (Straight and Cooper 2000).

The status of Chuck-will's-widow in the Bahama Islands remains unclear. The species is considered a rare to uncommon winter visitor (Brudenell-Bruce 1975, Emlen 1977, Buden 1987, White 1998, Straight and Cooper 2000). Northrop (1891) collected a male with enlarged testes during the breeding season (15 May) on Andros, but was uncertain of nesting. Paterson (1972) observed a bird incubating a single egg on Andros, but Bond (1973:3, 1984:20) rejected the record as a misidentified Antillean Nighthawk (*Chordeiles gundlachii*). However, Buden (1992) and Buden and Sprunt (1993) heard calling birds and flushed a pair during visits to several Exumas cays in April through June, suggesting possible breeding. Calling birds subsequently heard from February to July on several islands, documented in North American Birds seasonal reports, led to increased speculation of nesting. Breeding was eventually confirmed for Grand Bahama (Norton 1999; Norton and White 2001, 2002) and Abaco (Norton 2000). However, several questions remain unanswered. Were these breeding records extralimital, or indicative of larger breeding populations? If the latter, how large might these populations be, and how widespread are they?

The objective of our study was to clarify the population status of Chuck-will's-widow in the Bahama Islands. Our results, when compared to similar surveys from the species' continental range in the United States, provide inferences about the bird's abundance and breeding status.

METHODS

We conducted breeding season surveys on the three largest northern islands: North Andros, Grand Bahama, and Great Abaco. We followed generally practiced protocols for surveys of nightjars (e.g., Cooper 1981, Wilson 2008). Surveys were conducted along 8–20 km routes that included 9–12 brief stops (usually 10) of 2–5 min duration at 1 km or greater intervals. Surveys, with a few exceptions, were completed during >50% moon illumination. Surveys were conducted during either the hour before sunrise or within 1–2 hrs following sunset, depending on when the moon was above the horizon. Weather varied from clear to overcast but with relatively low wind and absence of rain. We recorded the

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GPS (Global Positioning System) coordinates, time, and number of calling birds for each stop. We broadcast a recording of the song by speaker or whistled a cruder imitation of the song by mouth for most stops. We did not differentiate between spontaneous and solicited calls, as both were frequently detected. Calling birds could at times be heard at >500 m; we tried not to double-count individuals on consecutive stops, but this may have resulted in slight underestimation bias.

We (MRP, VR, and EG) conducted seven surveys on North Andros during 2009. These included: 10 and 12 May (mornings) south of Nichol's Town; 17 May (morning) between Mastic Point and San Andros Airport; 2 June (evening) west of Stafford Creek; and 3, 4, and 5 June (evenings) between Stafford Creek and Love Hill. These routes traversed primarily Caribbean pine (*Pinus caribaea*) forest habitat with scattered openings, but coppice, marsh, and residential areas were present at some stops.

WKH conducted three surveys during 2007 on Grand Bahama. These included: 1 July (morning) from Bassett Cove to the oil storage facility east of Riding Point; 1 July (evening, 12 stops, no moonlight) near the water towers at Lucayan Estates; and 2 July (morning, 9 stops) in Lucaya along West Beach and Midshipman roads. All routes were in primarily pine forest with scattered openings; however, the first included occasional coppice and residential areas, and the third transected a rural residential area.

EDB conducted repeated surveys along two routes (9 stops each) between Treasure Cay and Leisure Lee on Great Abaco during 2009. These included four evening surveys on 5 May, 10 May (no moonlight), 1 June, and 5 June. Additional evening surveys repeated in July and August yielded no calling birds and were excluded from analysis. Routes included pine forest with some coppice. CS conducted two surveys in 2009 further south on Great Abaco. These were 14 July (morning) along Great Abaco Highway between Crossing Rocks and Abaco National Park, and 15 July (morning) along Mid Road towards Hole-in-the-Wall. The routes passed through pine forest with variable understory, and several stops included coppice.

We derived the following variables for each route: total number of calling birds; mean birds per stop along route; proportion of stops with bird detections; number of birds calling per occupied stop (with birds calling); and density (pairs/km^2). Numbers were adjusted for routes of 9 or 12 rather than 10 stops to reflect the standard 10-stop route (i.e., birds/stop multiplied by 10). We assumed that all calling individuals were detected within a 500-m radius to estimate population density (calling males = pairs/km^2). Thus, the number of calling birds detected at each stop corresponded to a minimum density of pairs per 0.785 km^2 (area of circle with 500 m radius). This assumption is subject to several factors influencing detection rate, including some birds being heard at greater distances and many individuals not calling during the brief stops.

RESULTS

We encountered 42 calling birds along the 14 survey routes (Table 1). The number of calling birds per 10-stop route varied from zero to 12.2. Calling birds were detected on four of the seven (57%) Andros routes and on 100% of the three Grand Bahama and four Abaco routes. Grand Bahama appeared to host the highest density of individuals. One nine-stop route through a rural residential area yielded 11 calling birds. The maximum number of calling birds recorded per stop was two, and this was consistent for all three islands. Three birds were heard at several stops on Grand Bahama but, in each case, one was judged to be a bird heard at the previous stop and was not counted.

Repeated surveys along two routes on Great Abaco illustrated nightly and seasonal variation. Calling birds after sunset numbered four (5 May), five (10 May), six (1 Jun), and seven (5 Jun) for the 18 stops of both routes combined. No birds were detected on three additional surveys (22 and 30 Jul, 5 Aug), and these surveys were excluded due to lateness of season. Our mean estimate of calling birds for the first four surveys (5.5) was 21% below the maximum count (7), suggesting detection of 79% or less for individual surveys.

DISCUSSION

Standardized surveys provide the best understanding of the relative abundance of Chuck-will's-widow, and only males are known to give the primary song (Straight and Cooper 2000). A number of factors can affect calling rates and influence detection rates and density estimates. Male calling peaks in late spring in continental populations and may decrease markedly in July (e.g., Cooper 1981, Straight and Cooper 2000). Both calling rate and duration of calling through-

TABLE 1. Chuck-will's-widows on North Andros (7 survey routes), Grand Bahama (3 routes), and Great Abaco (4 routes), Bahama Islands. Values include $\bar{x} \pm$ SD and range within parentheses for birds per 10-stop route and associated variables.

Island	Total stops	Total birds	Birds per route	Birds per stop	% stops with detections	Birds per occupied stop	Density (pairs/km^2)
North Andros	70	10	1.4 ± 1.4 (0–3)	0.14 ± 0.14 (0–0.3)	12.9 ± 12.5 (0–30)	1.0 ± 0.0 (1)	0.18 ± 0.18 (0–0.38)
Grand Bahama	31	16	5.6 ± 5.8 (2–12.2)	0.56 ± 0.58 (0.2–1.2)	38.3 ± 34.4 (17–78)	1.4 ± 0.3 (1–2)	0.71 ± 0.74 (0.25 ± 1.53)
Great Abaco[a]	38	16	3.0 ± 0.8 (1–5)	0.30 ± 0.08 (0.1–0.5)	24.6 ± 5.4 (20–32)	1.3 ± 0.5 (1–2)	0.38 ± 0.10 (0.13–0.64)

[a] Two routes were replicated four times; maximum counts were used to derive total birds and ranges, but average values from replicates were used in computing $\bar{x} \pm$ SD values.

out the night increase significantly with greater moonlight (Cooper 1981, Mills 1986, Wilson and Watts 2006, Woods and Brigham 2008).

Our surveys suggest a substantial breeding population of Chuek-will's-widows exists on the large northern islands in the Bahamas. Abundance varied locally, but ealling males were widespread on each of the large islands surveyed (North Andros, Grand Bahama, and Great Abaeo). Birds ealling in summer on New Providenee (e.g., Norton and White 2002) and the Exumas (Buden 1992, Buden and Sprunt 1993) suggest breeding populations on these islands as well.

Relative densities from our surveys ($\bar{x}$ = 0.14–0.56 birds/stop among the 3 islands) were generally lower than surveys within the primary range of continental populations. Cooper (1981), from 20 surveys in northern Georgia, reported 0-1.75 ealling individuals per stop ($\bar{x}$ = 1.37 for 6 nights with ≥0.5 lunar illumination). James and Neal (1986) listed eounts of 1.77 and 2.32/stop in Searcy and Clay eounties, Arkansas, respeetively. Baumgartner and Baumgartner (1992) reported counts of 1.67 and 1.98/stop in northeast and southeast Oklahoma, respectively. More reeently, Wilson (2008) reported on eoordinated surveys from seven states having two or more surveys conducted in 2007. These ineluded: Florida with 1.54 birds/stop, Alabama with 1.50, South Carolina with 1.30, Georgia with 0.98, Mississippi with 0.90, Virginia with 0.44, and North Carolina with 0.42. Our surveys differed somewhat from those of Wilson (2008) in that stops were spaced more closely and listening time was briefer. We also used tape playbaek or voeal imitation to help stimulate ealling.

We do not know whether the eurrent breeding population in the Bahama Islands represents a reeent colonization or has been overlooked. The relatively low densities compared to continental populations suggest either a lower earrying capaeity in the Bahama Islands or reeently established populations that have yet to reach carrying eapacity. Population densities at the expanding northern periphery of the continental range are generally low (Hunt 2008). Future surveys eould improve our knowledge on these possibilities. Two birds colleeted from Cuba during the breeding season with enlarged gonads suggest possible breeding there as well (Straight and Cooper 2000).

Our density estimates provide for a rough approximation of the total population in the

Bahamas. The estimates are limited by three major factors (see also Wilson 2008): (1) some birds were detected at distances >500 m, resulting in overestimation; (2) not all males present were calling, resulting in underestimation; and (3) survey routes may not have been representative of the habitats available on each island. We suspect our numbers are underestimates. We multiplied our estimates by the quantity of suitable habitat on each island based on detailed maps. As many as 214 pairs exist on Andros (0.18 pairs/km^2; 5,957 km^2 total area; 20% of total area assumed to be suitable habitat), 390 pairs on Grand Bahama (0.71 pairs/km^2; 1,373 km^2 total area; 40% suitable habitat), and 192 pairs on Abaco (0.38 pairs/km^2; 1,681 km^2 total area; 30% suitable habitat). New Providence (207 km^2) presumably hosts a breeding population, and smaller populations may exist on other islands. We conclude the Bahama Islands supports an aggregate population in the vicinity of 500–1,000 pairs.

Clearly, the recent scattered reports of singing and nesting birds reflect sizeable breeding populations rather than extralimital records. Efforts should be undertaken to locate additional populations on other islands and to examine whether populations are gradually increasing in size.

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Yellow Rails Wintering in Oklahoma

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ABSTRACT.—Yellow Rails (*Coturnicops noveboracensis*) were recently discovered to migrate through southeastern Oklahoma in small numbers during fall with a few records into December and a single record in January. We made seven trips (3 in Nov 2008 and 1/month from Dec 2008 through Mar 2009) to Red Slough Wildlife Management Area in McCurtain County (Oklahoma) to catch and band Yellow Rails. Twenty-five Yellow Rails were banded and birds were observed during each month. Rails were encountered in areas dominated by *Sporobolus* spp. averaging 44 cm in height in areas with 4 cm or less of standing water. Yellow Rails appear to overwinter in small numbers in McCurtain County, Oklahoma ~300 km north of the Gulf Coast. *Received 22 June 2009. Accepted 15 October 2009.*

Yellow Rails (*Coturnicops noveboracensis*) are secretive, nocturnal birds that breed in the northern United States and Canada with a disjunct population in southcentral Oregon (Bookhout 1995). The total population of Yellow Rails is estimated to be only 17,500 individuals (Butcher et al. 2007). The species is on the Audubon's Society's Red WatchList (Butcher et al. 2007) and is a species of special concern in Canada (Environment Canada 2006), and most of the states where breeding occurs (Grace et al. 2005). Yellow Rails generally leave breeding areas between mid-August and November (Stenzel 1982, Bookhout 1995, Popper and Stern 2000, Goldade et al. 2002) and winter along the coast, from Texas to North Carolina (Bookhout 1995). Several studies of Yellow Rails have been conducted in breeding areas but little is known about their migratory or wintering ecology (Bookhout 1995).

The first Yellow Rail recorded in Oklahoma was collected on 7 March 1842 in what is now Delaware County (Tomer 1959). More than a century passed before Yellow Rails were again reported in Oklahoma. In 1954, one was reported killed by a mowing machine (Heck and Arbour 2008). These authors summarized published dates of occurrence for the 20th century and reported one record from the 1960s, three records from the 1970s, no records during the 1980s, and four records from the 1990s. W. D. Arbour began conducting regular rope drags to flush Yellow Rails beginning in 2001 at Red Slough Wildlife Management Area (WMA) in McCurtain County, Oklahoma. Yellow Rails were observed annually at this location from 2001 to 2008 (Heck and Arbour 2008). They are now considered to be regular autumn migrants from 15 October through 26 November in southeastern Oklahoma (OBRC 2004).

Yellow Rails were also recorded during December in 2 years (2004 and 2005) at Red Slough WMA and a single record exists from January (2004) at this location (Heck and Arbour 2008). We hypothesized that Yellow Rails may overwinter in small numbers in southeastern Oklahoma given the species has been recorded as late as mid-January in McCurtain County.

METHODS

Red Slough Wildlife Management Area (33° 44′ 05″ N, 94° 38 13″ W; Fig. 1) is in McCurtain County, Oklahoma, and consists of ~1,000 ha of moist soil management areas, 1,160 ha of (reforesting) bottomland hardwoods, and 165.6 ha of reservoirs for a total of 2,325.6 ha (USDA 2009). Red Slough WMA is cooperatively managed by the U. S. Forest Service, Natural Resources Conservation Service, Oklahoma Department of Wildlife Conservation, and Ducks Unlimited (USDA 2009).

We traveled to Red Slough WMA seven times between November 2008 and March 2009 to capture and band Yellow Rails (3 times in Nov and once monthly from Dec through Mar). Vegetation was sampled at nine locations where birds were flushed during November 2008. A 1 × 1 m^2 frame was placed at each location where we flushed Yellow Rails and vegetation height of

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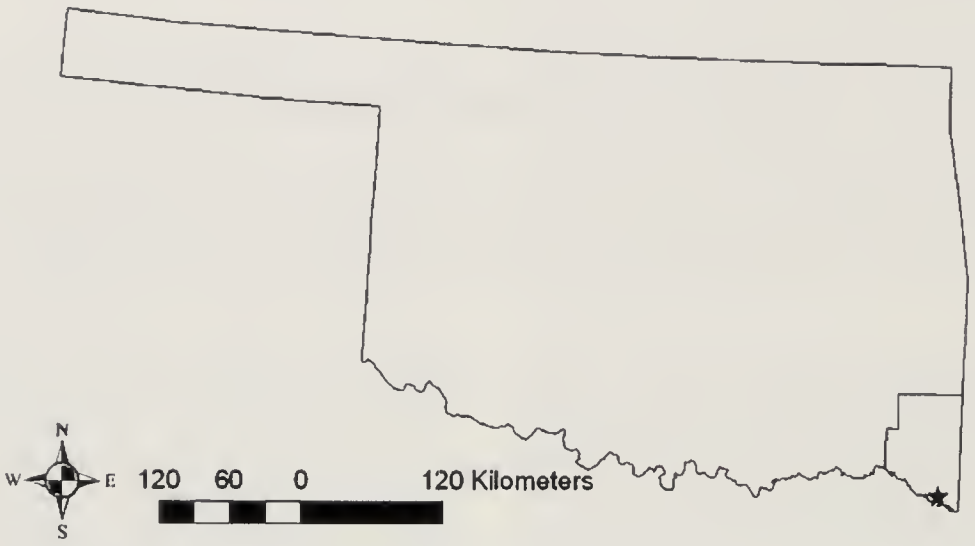

FIG. 1. Red Slough Wildlife Management Area (black star) in McCurtain County, Oklahoma.

each species was measured as well as percent cover following Daubenmire (1959). Yellow Rails may have run before flushing (which could potentially bias the results), but the habitat appeared to be homogeneous and any bias was expected to be minimal.

We began capturing Yellow Rails ~30 min after sunset and continued our efforts for 3 hrs each night. We used a 12-m nylon rope weighted with bottles (filled with rocks) which two people dragged through damp, grassy areas where rails had previously been encountered. Rope-dragging caused rails to flush and we were able to shine a handheld spotlight on the area where the bird landed and catch them in a small handheld net. Each bird was banded with a USGS aluminum band, classified to age following Pyle (2008), and released.

RESULTS

Twenty-five Yellow Rails were banded from November 2008 through March 2009 (Table 1). One bird banded in November 2008 was recaptured in December 2008 and one bird banded in December 2008 was recaptured in January 2009. A single Yellow Rail was flushed in February 2009 but we were unable to catch it. During November, most birds captured (9 of 13) were classified as adults (i.e., AHY) following Pyle (2008). In contrast, from December 2008 through March 2009, most birds captured (8 of 12) were classified as young (i.e., HY/SY).

TABLE 1. Trapping effort and captures of Yellow Rails, McCurtain County, Oklahoma, 2008–2009.

Month	# hours of sampling	New birds	Recaptures
November 2008	18	13	2 (both banded earlier in Nov)
December 2008	6	9	1 (banded in Nov)
January 2009	6	1	1 (banded in Dec)
February 2009	6	0	0
March 2009	6	2	0

Fourteen genera in eight plant families were identified in the nine vegetation plots. Seven plots were dominated by grasses (60–100% cover), mainly *Sporobolus* spp. (dropseed), some identified as *Sporobolus compositus*. Other grasses on these seven plots included *Steinchisma hians* (gaping grass) and *Panicum* spp. (panicgrass). One plot was dominated by flatsedge (*Cyperus* spp.) with 85% cover, and another by an unidentified Polygonaceae with 97.5% cover. Other plants encountered included *Ambrosia* spp. (ragweed), *Ammannia* spp. (toothcup), *Andropogon virginicus* (broomsedge bluestem), *Boltonia asteroides* (white doll's daisy), *Eleocharis* spp. (spike-rush), *Hypericum drummondii* (St. John's wort), *Juncus* spp. (rush), *Oxalis* spp. (wood sorrel), and *Tridens strictus* (long-spike tridens).

The dominant vegetation averaged (± SE) 44.1 ± 4.6 cm in height in areas where rails were captured. Ten Yellow Rails were captured in areas with no standing water and fifteen were captured in shallow water ≤4 cm deep.

DISCUSSION

Yellow Rails appear to winter in small numbers at Red Slough WMA in McCurtain County, Oklahoma. This is considerably farther north than previously reported wintering areas, because Red

Slough WMA is ~ 300 km north of the Gulf Coast. It is unknown whether this is a recent wintering range expansion or whether Yellow Rails have wintered here but not been previously detected. Most birds banded during winter (Dec–Mar) were HY/SYs, which suggests this species may undergo differential migration and young winter farther north than adults.

Yellow Rails are reported to use the drier areas of *Spartina* spp. marshes along the coast (Bookhout 1995). Radiotelemetry in coastal Texas suggested that Yellow Rails prefer areas dominated by saltgrass (*Distichlis spicata*) and gulf cordgrass (*Spartina spartinae*) (Grace et al. 2005). Wayne (1905: 396–397) collected wintering Yellow Rails near Charleston, South Carolina away from the immediate coast in a ''low, wet piece of open land with a dense growth of short, dead grass''. He collected 58 Yellow Rails between 1903 and 1918 at this freshwater locality (Post 2008). Heck and Arbour (2008) suggested Yellow Rails in Oklahoma occur primarily in fall panicum (*Panicum dichotomiflorum*) and longleafed rushgrass (*Sporobolus asper*) during fall migration. We generally found Yellow Rails in areas dominated by *Sporobolus* spp. rather than *Panicum* spp., although the number of higher taxa (families and genera) at our sites was fairly high. It is possible that Yellow Rails choose wintering habitat based on structural components (e.g., areas dominated by grassy vegetation <50 cm in height with little or no standing water) rather than by dominant plant genera, as suggested for other rail species (Conway 1995, Melvin and Gibbs 1996).

Yellow Rails are difficult to detect and may winter farther inland than previously reported. Given that they overwinter in small numbers in southeastern Oklahoma, observers elsewhere in the southeastern United States should be alert for the possibility of Yellow Rails overwintering in damp grassy areas.

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Breeding of the Giant Laughingthrush (*Garrulax maximus*) at Lianhuashan, Southern Gansu, China

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ABSTRACT.—We describe the nest sites, nests, eggs, and incubation and provisioning behavior of the endemic Giant Laughingthrush (*Garrulax maximus*) in a coniferous forest (2,850–2,950 m asl) at Lianhuashan, southern Gansu, central China. We found seven shallow bowl-shaped nests in *Picea-Abies* trees, 4.0 ± 1.5 m ($\bar{x}$ ± SD, n = 7) above the ground during May and June 2003, 2007, and 2008. Clutch size was 2.2 ± 0.4 unspotted blue eggs (2–3, n = 6) of which 1.4 ± 0.5 nestlings hatched (1–2, n = 7), and 1.0 ± 1.0 young fledged (0–2, n = 7). Three nests failed, possibly due to predation or abandonment during prolonged rainfall. Both males and females incubated clutches; nest attentiveness during the day decreased from 92.6 ± 0.9% before hatching to 59.4 ± 1.5% during days 3–7 of the nestling period. Both parents fed the nestlings (1.0 ± 1.0 times/hr) and consumed the feces (0.3 ± 0.5 times/hr) during the 7–15 days after hatching *Received 28 March 2009. Accepted 26 October 2009.*

The endemic Giant Laughingthrush (*Garrulax maximus*) is distributed from southern Gansu and southeastern Qinghai to southern and southeastern Tibet and northern Yunnan in southern and central China (Zheng 2005, Thompson 2007). Habitats occupied include open broadleaf and mixed broadleaf-coniferous forests, bamboo (*Phyllostachys* spp.) scrub in broadleaf evergreen forest, oak (*Quercus* spp.) forest with scattered conifers, and relatively open broadleaf evergreen forest with shrub understory at 2,135–4,115 m elevation (Thompson 2007).

The Giant Laughingthrush is the largest laughingthrush (Cheng et al. 1987, Rasmussen and Anderton 2005) and was previously treated as a subspecies of Spotted Laughingthrush (*G. ocellatus*) (Ali and Ripley 1996). Little is known about its natural history and breeding except one description based on a single nest in a bamboo clump, which contained two eggs (Ludlow and Kinnear 1944). We describe the nests, eggs, nestlings, and nesting behavior of this species in an alpine conifer-dominated forest in southern Gansu, China.

METHODS

Study Area.—Our study area was in the Lianhuashan Nature Reserve (34° 57′ N, 103° 46′ E) in southern Gansu Province, China. The forested area occurs on north, northeast, and northwest-facing slopes; only shrubs and grasses grow on south-facing slopes. Coniferous forest is the most prevalent cover type and is dominated by Dragon spruce (*Picea asperata*) and Farges fir (*Abies fargesii*). The other cover types are: (1) coniferous-deciduous forest, including spruce, fir, Himalayan birch (*Betula utilis*), and willow (*Salix* spp.); and (2) shrublands including willow, sea buckthorn (*Hippophae rhamnoides*), and barberry (*Berberis* spp.). The study area has been described by Sun et al. (2003). The mean annual temperature is 5.1–6.0° C, with a maximum of 34.0° C and minimum of −27.1° C. The climate is semiarid, and the annual precipitation is about 65 cm.

Field Procedures.—We located seven nests (6 during incubation and 1 during the nestling stage) by following nesting-related activities of adults or by systematically checking individual trees in the conifer-dominated forest between 2,850 and 3,100 m elevation during three breeding seasons (Apr–Jul in 2003, 2007, and 2008). We inspected nests every 3–5 days to identify hatching and fledging dates and, if possible, cause of nest failure.

Incubation or brood care was documented using data loggers (Tinytag Plus 2 Gemini Data Loggers, West Sussex, UK) at two nests, one of which was monitored for 194 hrs during 11 days. The probe was placed among the eggs to take a temperature reading every 15 sec. Length of on- and off-nest bouts, and behaviors of provisioning

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TABLE 1. Giant Laughingthrush nests observed in the Lianhuashan Nature Reserve, southern Gansu, central China during May and June 2003, 2007, and 2008. DBH = diameter at breast height.

			Nest tree		Nest		Clutch size			
Nest #	Date found	Stage	Species	DBH (cm)	Height above ground (m)	Distance to the trunk (m)	Eggs	Nestlings	Fledglings	Nest fate
1	25 May 2003	Incubation	Spruce	12	7.0	0.40	3	2	2	Successful
2	27 May 2003	Incubation	Spruce	10	3.0	0.04	2	2	2	Successful
3	9 June 2003	Nestling	Spruce	14	4.5	0.10		2	2	Successful
4	24 May 2007	Incubation	Fir	32	3.8	2.00	2	1	1	Successful
5	9 June 2007	Incubation	Spruce	13	4.0	0.05	2	1	0	Abandoned
6	26 May 2008	Incubation	Fir	45	2.4	2.10	2	1	0	Depredated
7	3 June 2008	Incubation	Spruce	26	3.5	2.20	2	1	0	Depredated

young and removing feces were recorded at one nest by observation (33.7 hrs during days 6–10, 12–13, and 15 of the nestling period) and at another nest by video recorder (1.9 hrs on the 15th day of the nestling period). All observers and equipment were camouflaged using branches and leaves.

Nest characteristics were measured after termination of nesting and included height of the nest, distance of the nest to trunk, and height and diameter at breast height (DBH) of the nest tree. All data are expressed as $\bar{x} \pm$ SD.

RESULTS

Nests were placed in Dragon spruce or Farges fir with three in branches of large conifers (DBH = 34 ± 10 cm) at a height of 2.4–3.8 m above ground and 2.0–2.2 m from the trunk. Four nests were in small spruce (DBH = 12 ± 2 cm) nearly touching the trunk at a height of 3.0–7.0 m

FIG. 1. Nest with two eggs of the Giant Laughingthrush in a Dragon spruce (*Picea asperata*) at Lianhuashan, southern Gansu, central China. Photograph by Chenxi Jia.

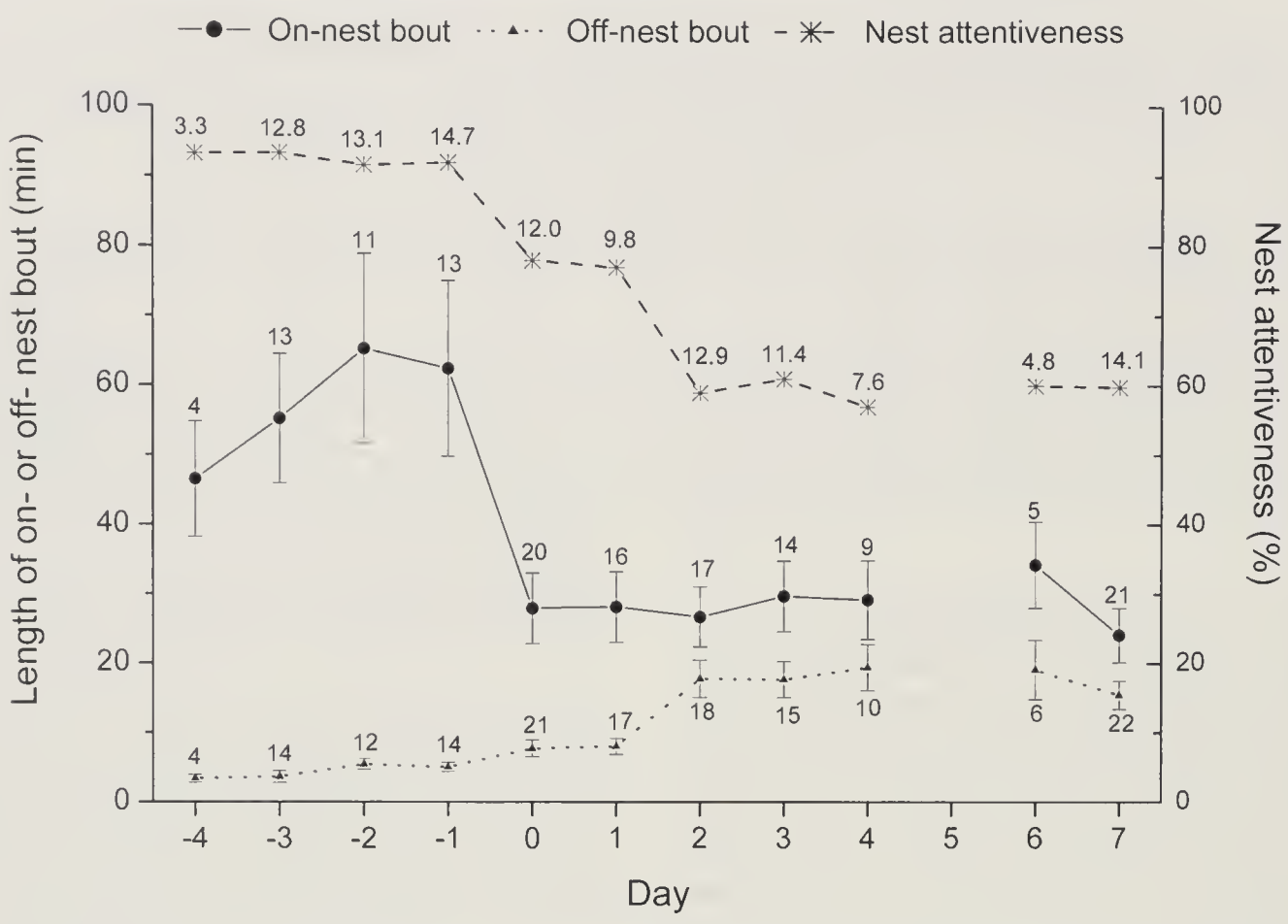

FIG. 2. Length of on- and off-nest bouts and nest attentiveness of the Giant Laughingthrush at one nest (found in 2007) during the incubation and nestling periods. Day 0 = hatching day. The numbers on the asterisks are the time (hrs) monitored by data loggers whereas the numbers on/under the bars are the sample sizes of on/off-nest bouts.

(Table 1). Nests were shallow and bowl-shaped (Fig. 1) with an inside diameter of 11.6 ± 0.7 cm (10.8–12.2 cm, $n = 4$), outside diameter of 19.3 ± 0.9 cm (18.5–20.0 cm), inside depth of 5.1 ± 1.3 cm (4.0–6.5 cm), and outside height of 9.4 ± 1.1 cm (8.0–10.5 cm). Two nests were 78 and 80 g in wet weight, respectively. The inside bowl of the nest was lined with thin strands of bamboo, madder (*Rubia* spp.), and spiraea (*Spiraea* spp.) stems, whereas the outer bowl and foundation were mainly of twigs, 25 cm (10–38 cm) in length, mostly of honeysuckle (*Lonicera* spp.) with a few from spruce, fir, and birch.

Clutch size was 2.2 ± 0.4 eggs (2–3, $n = 6$) with 1.4 ± 0.5 nestlings hatched ($n = 7$) and 1.0 ± 1.0 young fledged ($n = 7$). Ten unspotted blue eggs were 33.5 ± 1.5 mm (31.6–36.2 mm) in length, 22.9 ± 0.7 mm (21.6–24.4 mm) in diameter, and 8.8 ± 0.8 g (7.8–10.0 g) in weight. One nest was abandoned in the nestling stage, possibly due to prolonged rainfall (15–22 Jun 2007). One nest was possibly predated as one egg had a small hole in the eggshell during the incubation stage. The other nest was predated at 2344 hrs (Beijing Time, revealed by data logger) during the nestling stage with the nest overturned and feathers of the adult scattered on the ground.

Mean length of on-nest bouts decreased from 59.4 ± 39.1 min (1.5–136.0 min) before hatching to 27.6 ± 18.0 min (3.0–72.5 min) during the nestling period, whereas mean off-nest bouts increased from 4.6 ± 2.8 min (0.5–10.5 min) to 15.6 ± 10.1 min (2.5–45.0 min) (Fig. 2). Nest attentiveness during the day decreased from 92.6 ± 0.9% before hatching to 59.4 ± 1.5% during days 3–7 of the nestling period. The female began diurnal activities at 0613 hrs (±28 min, $n = 9$) and began nocturnal brooding at 1931 hrs (±28 min, $n = 9$).

Both parents provisioned nestlings and removed (or consumed) feces at a frequency of 1.2 ± 1.5 (0–6) and 0.5 ± 0.9 (0–3) times/hr, respectively, based on observation (32 hrs) and video recording (1.9 hrs) during days 7–15 of the nestling period. The nestling period appeared to be 17–18 days (2 nests).

DISCUSSION

Nests in conifers were higher than the nest in the bamboo clump (1.2 m) reported by Ludlow and Kinnear (1994) and the nest of the Spotted Laughingthrush (<2 m) (Ali and Ripley 1996). Nest materials used by the Giant Laughingthrush were similar to those used by the closely related Snowy-cheeked Laughingthrush (*G. sukatschewi*) (Bi et al. 2003) and the Spotted Laughingthrush (Ali and Ripley 1996), but did not include moss, birch leaves, or strips of honeysuckle bark, which are frequently used by the Elliot's Laughingthrush (*G. elliotii*) (Jiang et al. 2007). We did not find nests in bamboo clumps, which were quite short (<1.8 m) and scattered under the conifer trees or in small patches within the forest. The bamboo in this area had been nearly clear-cut by the local people 5 years earlier.

The unspotted blue color of the eggs was similar to the Snowy-cheeked Laughingthrush (Bi et al. 2003) but possibly differed from the Spotted Laughingthrush, which has eggs that are spotless or with a few chocolate-brown specks near the broad end (Ali and Ripley 1996). Mean clutch size was similar to that of the Spotted Laughingthrush (normal = 2 eggs, Ali and Ripley 1996), but less than the high-altitude Brown-cheeked Laughingthrush (*G. henrici*) (2.6 eggs, Lu et al. 2008), Snowy-cheeked Laughingthrush (3.5 eggs; Jie Wang, unpubl. data), and Elliot's Laughingthrush (3.4 eggs, Jiang et al. 2007).

Both parents incubated eggs and brooded nestlings, similar to most other laughingthrushes (Thompson 2007). Frequency of provisioning nestlings was lower than for the Snowy-cheeked Laughingthrush (1.2 vs. 7.9 times/hr; Bi et al. 2003). One reason may be that adult Giant Laughingthrushes seemed to be vigilant and prone to decrease their activities during the nestling stage, as the frequency of provisioning young estimated from video recordings (7 times in 1.9 hrs) was higher than from observation (31 times in 32 hrs).

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First Description of the Nest of Jocotoco Antpitta (*Grallaria ridgelyi*)

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ABSTRACT.—The Jocotoco Antpitta (*Grallaria ridgelyi*) is an endangered and poorly studied inhabitant of montane bamboo (*Chusquea* spp.) thickets of extreme southeastern Ecuador. There is nothing known of the breeding biology of Jocotoco Antpitta apart from a single record of a dependent juvenile, and we describe a nest of this species for the first time. The nest was a bulky cup composed primarily of dead plant materials and firmly supported by a large clump of epiphytes on the side of a dead trunk. The single nestling was provisioned at a rate of 1.96 feedings/hr during the final 5 days prior to fledging. Two adults brought food to the nestling, often delivering prey from a nearby worm-feeding station created by the Jocotoco Foundation. The pair we studied may breed twice a year, but this may have been facilitated by their proximity to the artificial feeder. *Received 1 May 2009. Accepted 17 September 2009.*

The Jocotoco Antpitta (*Grallaria ridgelyi*) is one of the rarest species of this poorly known genus that encompasses 31 species in the family Grallariidae (Remsen et al. 2009). Despite its large size and distinctive plumage, the Jocotoco Antpitta was only described 10 years ago (Krabbe et al. 1999), having been overlooked due to its propensity to forage in the thick undergrowth of *Chusquea* bamboo-covered slopes (Krabbe et al. 1999, Ridgely and Greenfield 2001, Heinz et al. 2005, Freile et al. 2010). The Jocotoco Antpitta is apparently confined to southeastern Ecuador and is considered Endangered by BirdLife International (2009). The breeding biology of the Jocotoco Antpitta remains undocumented with only a single description of a juvenile accompanying two adults (Greeney and Gelis 2005b). We describe the first nest of Jocotoco Antpitta from the Tapichalaca Biological Reserve in southeastern Ecuador.

METHODS

We made all observations at the Tapichalaca Biological Reserve (04° 30′ S, 79° 10′ W) near Valladolid in extreme southeastern Ecuador. The terrain is typically steep for this elevation in the Andes (~ 2,500 m) with vegetation characterized by high epiphyte density, a canopy height of 15–30 m, and a dense understory comprised largely of *Chusquea* bamboo (Krabbe et al. 1999). We made nest measurements to the nearest 0.5 cm and behavioral observations at the nest using a tripod-mounted video camera placed ~ 5 m from the nest. We recorded 16.3 hrs of video from 1030 to 1800 hrs on 10 November 2008 (5 days prior to fledging) and from 0700 to 1715 hrs the day before fledging.

RESULTS

We observed two adult Jocotoco Antpittas on the morning of 5 November 2008 gathering food items at the worm feeder and black-light trap adjacent to the Tapichalaca Lodge (~ 2,500 m asl). Adults carried multiple invertebrates from this feeding area, leaving in the direction of the subsequently discovered nest. We again observed adults carrying prey in the same direction on 6 November.

On 8 November 2008 at 1000 hrs MEJ found the nest, 30 m from the feeders, which contained a single large nestling. The nestling was well feathered at the time of discovery, cinnamon on the back, chestnut on the crown and upper breast, and finely barred with black on all visible areas (Fig. 1). Most of the ocular area was still bare with just a faint hint of the white malar pattern of adults. The upper mandible was dark with a pale orange tip while the lower mandible was mostly dull orange. The gape was orange but we did not examine the mouth lining or remove the nestling for closer inspection of plumage patterns. The nest was 3.6 m above the ground on the side of a vertical, rotting tree trunk that was 4.1 m tall

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FIG. 1. Nestling Jocotoco Antpitta (*Grallaria ridgelyi*) in southeastern Ecuador, 3 days prior to fledging (Photograph by M. E. Juiña).

FIG. 2. Nesting site of Jocotoco Antpitta (*Grallaria ridgelyi*) in southeastern Ecuador. The white arrow points to the nest itself (Photograph by M. E. Juiña).

(56 cm dbh) (Fig. 2). The nest was placed flush against the trunk and was supported primarily by a cluster of *Tillansia* bromeliads and secondarily by a 4-cm diameter, horizontal branch crossing under the nest. The nest was a large cup comprised predominantly of dead plant materials, mostly dicot and bromeliad leaves. The cup was lined internally with a thick layer of fine black rootlets and bare fern rachises.

Internal measurements of the nest cup were 15.5 × 14.0 cm in width (measured at perpendicular angles) and 12.5 (back) to 17.0 cm (front) deep. Externally, the nest was 23.5 by 26 cm in diameter and 18 cm tall. The area around the nest contained a dense understory and, along with the dense ~ 20 m canopy, provided nearly 90% shading of the nest. The nest was directly shaded, predominantly by *Chusquea* bamboo, as well as epiphytic ferns and orchids. The nest was on the northeast side of the trunk on a northeast facing slope where it received most of its sun in the mornings.

Transcriptions of video at the nest revealed the nestling was brooded for only 7% of daylight hours. We were unable to ascertain if more than one adult brooded, but we confirmed that two adults brought food. Adult feeding visits to the nest were brief (mean ± SD = 2.2 ± 7.5 min), during which time they frequently probed sharply or rapidly into the nest lining. The nestling was provisioned at a rate of 1.96 feedings/hr with absences from the nest lasting 29.7 ± 24.4 min. The nestling often followed the adults to the rim of the nest as they left after delivering food during the day prior to leaving the nest. In the absence of adults, the nestling frequently stood and stretched its wings or shuffled about inside the nest, occasionally pecking at small invertebrates moving around the nest.

DISCUSSION

The nest of Jocotoco Antpitta is a deep, bulky cup similar in form to the described nests of other *Grallaria* (Greeney et al. 2008). The nest was well supported by bromeliads, against the trunk and branch of a dead tree, most similar to the nest situations of Rufous Antpitta (*G. rufula*) (Greeney

and Gelis 2005a), White-bellied Antpitta (*G. hypoleuca*) (Price 2003), Yellow-breasted Antpitta (*G. flavotincta*) (Greeney et al. 2009), Variegated Antpitta (*G. varia*) (Protomastro 2000), Pale-billed Antpitta (*G. carrikeri*) (Wiedenfeld 1982), Great Antpitta (*G. excelsa*) (Koefed and Auer 2004), and some Scaled Antpitta (*G. guatimalensis*) (Dobbs et al. 2001, 2003). The nest was composed predominantly of dead plant material, most similar to nests of Chestnut-naped Antpitta (*G. nuchalis*) (Juiña et al. 2009), Chestnut-crowned Antpitta (*G. ruficapilla*) (Martin and Greeney 2006), Plain-backed Antpitta (*G. haplonota*) (Greeney et al. 2006), Watkins's Antpitta (*G. watkinsi*) (Martin and Dobbs 2004), Variegated Antpitta (Quintella 1987, Protomastro 2000), Pale-billed Antpitta (Wiedenfeld 1982), and White-bellied Antpitta (Price 2003), as well as some nests of Moustached Antpitta (*G. alleni*) (Freile and Renjifo 2003, Londoño et al. 2004, Greeney and Gelis 2006), and Scaled Antpitta (Miller 1963; Rowley 1966; Dobbs et al. 2001, 2003).

Previous observations of an older, dependent fledgling Jocotoco Antpitta (Greeney and Gelis 2005b) were made on 30 November 2003 (HFG, unpubl. data). We also observed young fledglings accompanying adults to the worm feeder on multiple days in July and November 2007 and in April 2008. Observations of juveniles, with the exception of the previously published report of Greeney and Gelis (2005b), were all near the worm feeder maintained by the Jocotoco Foundation which is presumably visited by only one pair of Jocotoco Antpittas (MEJ, pers. obs.). These records suggest at least two broods a year. The effects of these feeders are unstudied despite the many birding lodges in Ecuador that now use worm feeders for *Grallaria* antpittas. We believe it is possible the year-round surplus of food provided by the feeders in our study area may have encouraged this pair of Jocotoco Antpittas to reproduce throughout the year, a pattern which may not be common for pairs without dietary supplementation. The importance of this possibility and the long-term repercussions on adult longevity and health deserve further study at this site and at others where worm feeders are used.

Clutch size remains undocumented for Jocotoco Antpitta, but repeated sightings of single fledglings (Greeney and Gelis 2005b, this study) combined with our observations of a single nestling, suggest this species may lay a smaller clutch than most other *Grallaria* (Greeney et al. 2008). Alternatively, single fledglings may reflect brood or clutch reduction from the typical two-egg clutches of the genus (Greeney et al. 2008).

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Nesting Ecology of the Grey-backed Shrike (*Lanius tephronotus*) in South Tibet

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ABSTRACT.—We studied the breeding ecology of the Grey-backed Shrike (*Lanius tephronotus*) in alpine shrub habitats in south Tibet. Shrikes nested between late May and early July at elevations of 4,010–4,540 m with a delay in nesting time with increased elevation. Nests were built mostly in bushes (83%), 0.7–2.1 m above ground. Clutch size averaged (± SD) 4.12 ± 0.67, range = 3–5 eggs and was smaller for pairs that nested later at higher elevations. Incubation by females began before clutch completion and lasted 15–18 days. Nestlings were cared for by both parents for 14–15 days. Breeding success, considered as the number of nest attempts that fledged at least one young, was 45.8%. Shrikes nesting in alpine habitats, compared with their lowland congeners, experienced shorter breeding seasons, produced fewer broods, smaller clutches, and larger eggs. They followed a life history strategy that allowed them to compensate for reduced annual fecundity under harsh conditions. *Received 29 June 2009. Accepted 1 November 2009.*

Lanius shrikes occur throughout the world except for South America and Australia (Lefranc and Worfolk 1997). Among the world's *Lanius* species, the Grey-backed Shrike (*L. tephronotus*) breeds at the highest elevations in the Himalayas on the Tibetan plateau, and peripheral zones at elevations of 2,700 to 4,500 m. This species is a partial migrant and most shrikes winter at low elevations between 300 and 2,500 m within their

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breeding range while a few migrate to lowland Southeast Asia (Lefranc and Worfolk 1997). However, little information pertaining to its reproduction has been published (Tsering et al. 2002). We studied the breeding ecology of the Grey-backed Shrike in a shrub-covered alpine valley in south Tibet. Our objectives are to report on the adaptation of life history traits of shrikes to high-elevation environments, and provide baseline data for species conservation.

METHODS

Study Area.—Field data were gathered in the Xiongse Valley (29° 27′ N, 91° 40′ E) near Lhasa, Tibet during 1996 and 1999–2004. Shrub vegetation characterizes the study area, including roses (*Rosa sericea*) and barberries (*Berberis hemleyana*) at 3,980–4,550 m, and Wilson junipers (*Sabina pingii*) at 4,550–4,980 m on south-facing slopes; spiraeas (*Spiraea japonica*) at 4,200–4,400 m, rhododendrons (*Rhododendron nivale*), and alpine willows (*Salix sclerophylla*) at 4,400–5,100 m on north-facing slopes.

Field Procedures.—Our study site was a 400-ha plot that covered the entire elevational range of the shrub vegetation. All Grey-backed Shrike nests located were described, and nest contents measured. Subsequent visits were made to examine nesting success. Several nests were checked infrequently because of their remoteness. We pooled the data of all years for analysis because of the small number of nests found during the study period. We chose $P < 0.05$ as the minimum acceptable level of statistical significance. Means are expressed ± SD.

RESULTS

Gray-backed Shrikes are the only *Lanius* species in Lhasa area. They arrived in the valley at 4,400 m in early May (2 to 12 May), singly (40% of 15 sightings) or in pairs (60%). Most departed by early October, but a few individuals were occasionally seen above 4,200 m until mid-December.

Nesting elevations ranged between 4,010 and 4,540 m with 69% (25 of 36 nests) below 4,300 m. Shrikes tended to nest near streams (<50 m; 61% of 36 nests). A 182-ha plot on south-facing slopes was systemically searched and seven shrike nests were found, producing a breeding density of 3.8 pairs/100 ha.

Shrikes nested in several plant species, of which most (61%) were in the two most common species, roses and barberries. Shrike nests constructed in bushes were nearer the ground (1.5 ± 0.4 m, range = 0.7–2.1, $n = 30$) than those in trees (2.8 ± 0.2 m, range = 2.5–3.0, $n = 6$; $t = 7.26$, $P < 0.001$). Individual bushes selected for nesting had dense foliage. Mean vegetation cover around shrike nests was 34 ± 18% (range = 10–85, $n = 30$), similar to the overall coverage (36%) in the study area. However, a few shrike nests were built in solitary tall bushes. Nests were cup-shaped and materials in the exterior layer of the nest cup consisted of thin twigs and roots of bushes. The interior layer consisted of feathers, sheep hair, and, at times, moss. Dimensions of seven nests were: exterior diameter 14.6 ± 0.9 cm (range = 13–16), interior diameter 9.0 ± 0.8 cm (range = 8–10), inside depth 6.8 ± 1.4 cm (range = 5–8.6), and outside height 15.3 ± 2.1 cm (range = 12–19).

Females did not lay eggs immediately after they finished building the nest. The duration between completion of nest construction and laying of the first egg was 6 to 10 days ($n = 5$ nests). Egg-laying began in late May and ended by early July with a peak in early June (Fig. 1). Shrikes nesting at higher elevations initiated clutches later than those nesting at lower elevations ($r = 0.41$, $n = 32$, $P = 0.02$).

One egg was laid per day ($n = 13$ daily monitored eggs from 6 nests). Eggs were whitish with light-brown spots, especially on the large end. Fresh mass of 11 eggs was 5.0 ± 0.16 g (range = 4.7–5.2). Measurements of 46 eggs from 12 nests averaged 25.7 ± 1.17 mm (range = 23.8–28.2) in length and 18.6 ± 0.48 mm (range = 17.8–20.0) in breadth. Clutch size varied from three to five eggs (4.12 ± 0.67, $n = 25$) with four being most common (56%). We detected a strong decline in clutch size over the season ($r = -0.43$, $n = 25$, $P = 0.03$). However, it was not significant once we controlled for elevation (partial correlation coefficient, $r = -0.28$, $n = 22$, $P = 0.18$). Clutch size decreased significantly as elevations increased ($r = -0.46$, $P = 0.02$), but did not if we considered the egg-laying time (partial correlation coefficient, $r = -0.34$, $P = 0.11$). The decrease of clutch size was affected by both breeding date and nesting elevation.

Incubation, considered as the period from the laying of the last egg to hatching of the first egg, started before clutch completion ($n = 6$ nests, 3 began with the first egg, 2 with the second egg, and 1 with the third egg). Only females incubated;

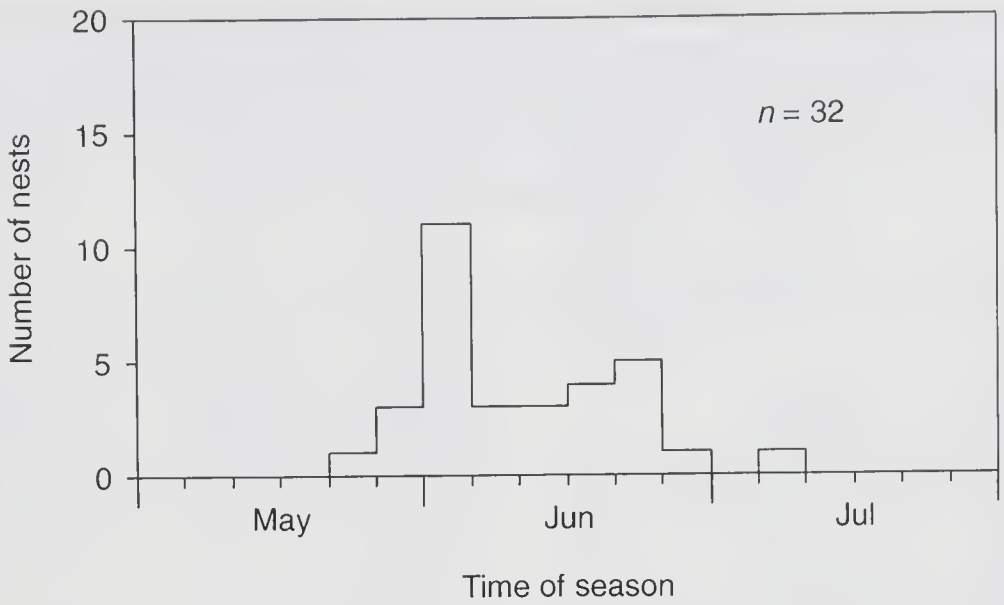

FIG. 1. Temporal distribution (all data combined) of date of laying of the first egg by Grey-backed Shrikes in the Xiongse Valley, south Tibet. Clutches initiated are arranged in 5-day periods.

incubation lasted 15 days at 4,050 m ($n = 1$) and 17–18 days at >4,350 m ($n = 3$). Males defended the nest during incubation and, at times, fed incubating females. Nestlings were provisioned by both female and male parents. Fledging occurred at 14–15 days (14.3 ± 0.6, $n = 3$) of age and fledglings weighed 34.3 ± 0.6 g (range = 32.2–36.9, $n = 6$), which was 71% of the adult female weight (48.1 g, average of 4 birds measured in the field).

Fifty of 58 eggs (86.2%) from 14 clutches hatched successfully, resulting in a brood size of 3.71 ± 1.00 ($n = 14$). Thirty of 33 hatchlings (90.0%) from nine clutches survived to fledging. Brood size at fledging was 3.36 ± 0.81 ($n = 11$). Overall breeding success, measured as the percentage of clutches that produced at least one fledged young, was 45.8% (11 of 24 known-fate attempts). The probability of a nest being successful calculated using Mayfield's (1975) method was 0.455 (i.e., 45.5%). Two (15.4%) of 13 failed attempts were due to nest abandonment because of inclement weather (nestlings died in the nest after continuous rainfall), and 11 (84.6%) because of predation (damaged nest structure) likely by mountain weasels (*Mustela altaica*), the most common carnivore in alpine areas.

DISCUSSION

Grey-backed Shrikes, compared to their Lhasa counterpart and other lowland congeners (Table 1), had a short breeding season (~ 50 days). They produced fewer and smaller clutches but larger eggs than their lowland relatives. Alpine shrikes had average clutch size similar to conspecifics in lowland Lhasa, but their maximum clutch size was one egg less. Shrike clutches within the alpine valley became smaller with increasing elevations. Invertebrates in the Tibetan plateau are scarce in terms of species diversity and population abundance decreases with increased elevations (Wang et al. 1992). Poor food availability could prevent shrikes nesting at high elevation from producing larger clutches. Selection should cause high-elevation shrikes to allocate more energy for each individual offspring (fewer but larger eggs) to improve their survival in harsh unpredictable alpine environments, which may compensate for reduced fecundity resulting from both fewer and smaller clutches. The shift in reproductive investment from offspring number toward offspring quality follows the general trend in avian life history shifts along elevational gradients (Badyaev 1997, Badyaev and Ghalambor 2001, Lu 2005, Bears et al. 2009). Badyaev and Ghalambor (2001) suggested that high-elevation birds provide greater parental care to their offspring in terms of longer incubation and nestling periods than their low-elevation counterparts. Grey-backed Shrikes nesting in alpine habitats versus lowland Lhasa had longer incubation and nestling periods (Table 1). Relative to other species of shrikes at the same latitude, Grey-backed Shrikes appeared to not be typically longer in these two parameters of parental care. This differentiation might be related to interspecific difference in body size or other traits.

TABLE 1. Life history parameters of some *Lanius* shrikes nesting near 30° N.

	L. tephronotus	*L. tephronotus*	*L. excubitor*	*L. ludovicianus*	*L. schach*
Locality	Lhasa, China	Lhasa, China	Sede Boqer, Israel	Florida, USA	Yangzhou, China
Latitude, N	29° 27′	29° 32′	30° 52′	27° 05′	32° 23′
Elevation, m	4,300	3,650	475	11	10
Breeding season length, days	50	65	120	160	100
Broods per year	1	1	1–4	1–3	1–2
Clutch size (range)	4.1 (3–5)	4.0 (3–6)	5.8 (5–7)	4.3 (2–6)	5.9 (4–8)
Egg volume, mm^3	8,916		10,153	8,689	8,484
Egg volume/female body mass	196		161	183	149
Incubation period, days (range)	16.7 (15–18)	15.3	16.8 (14–18)	17	14.0 (12–15)
Nestling period, days (range)	14.3 (14–15)	12.9	17.2 (16–19)	15	12.5
Source	This study	Tsering et al. 2002	Yosef 1992	Yosef 2001	Yan and Ma 1991, Hu et al. 2007

Grey-backed Shrike nests were intermediate in probability to be successful (45.5%), compared with those of other species of shrikes (Red-backed Shrike [*L. collurio*]: 35.3%, Horvath et al. 2000; Woodchat Shrike [*L. senator*]: 63.8%, Talagi 2001; Loggerhead Shrike [*L. ludovicianus*]: 60.0%, summarized by Yosef 2001). High-elevation shrikes, despite presumably higher juvenile survival, had lower annual productivity as a result of fewer and smaller clutches, and relatively low nesting success. This suggests that this species is more at risk if their habitats are altered by changes in land management activities or climate.

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The First Reported Hybridization of Abert's and Canyon Towhees (*Pipilo* spp.)

R. Roy Johnson[1,3] and Steven L. Hopp[2]

ABSTRACT.—Two mixed pairs of towhees were found in irrigated desert yards near Tucson, Arizona. The first known towhee F_1 hybrids, from a female *Pipilo aberti* (Abert's Towhee) and male *P. fuscus* (Canyon Towhee) were studied from winter of 1998–1999 through summer 2000. This mixed pair raised at least eight young in three broods during the two breeding seasons. Young were so similar to *P. fuscus* that, if seen outside this context, they would probably not be identified as hybrids. A second mixed pair, also near Tucson, suggests that hybridization between *P. aberti* and *P. fuscus* may be more common than originally thought. Lack of previously reported hybridization between *P. aberti* and *P. fuscus* may be either due to internal or external isolating mechanisms, limited survival and longevity, or human failure to recognize hybrids. *Received 2 September 2009. Accepted 10 January 2010.*

Hybridization among birds is relatively common, occurring in an estimated 10% of non-marine species (Grant and Grant 1992). The tendency to cross can be strong for some species pairs. For example, hybridization is common in three of the four species of "red-eyed" towhees (*Pipilo* spp.) of the United States and Mexico (Sibley 1954; Sibley and West 1958, 1959; Sibley and Sibley 1964; Greenlaw 1996). Hybridization has not previously been reported in the complex of four species of towhees collectively known as "brown towhees." The California Towhee (*P. crissalis*) of the Pacific West does not occur sympatrically with the other three species of "brown towhees." However, *P. fuscus* (Canyon Towhee) occurs throughout a portion of its range with both *P. aberti* in western Arizona and extreme northwestern Mexico, and with *P. albicollis* (White-throated Towhee) of central Mexico (Davis 1951, Johnson and Haight 1996, AOU 1998). *P. aberti* and *P. fuscus* occur together throughout much of the range of *P. aberti* in southern and central Arizona, but *P. aberti* occurs in more mesic riparian bottoms (Tweit and Finch 1994) while *P. fuscus* generally inhabits adjacent riparianlands or drier uplands (Johnson and Haight 1996).

OBSERVATIONS

SLH discovered a mixed pair of "brown towhees" nesting on Tanque Verde Creek during February and March 1999, ~24 km east of Tucson. The immediate area represents an ecotone between the riparian mesquite (*Prosopis velutina*) bosque (woodland) along Tanque Verde Creek, typical *P. aberti* habitat, and upland Sonoran desertscrub, habitat often occupied by *P. fuscus*. This mixed pair of towhees raised at least three broods of F_1 hybrids during the next two breeding seasons (Appendix).

The Abert's Towhee was observed on 16 April 1999 carrying nesting material into a 3.4 m tall ornamental juniper (*Juniperus* spp.). The Abert's Towhee was followed closely by the Canyon Towhee, suggesting the Abert's was the female because the male of a mated pair of Canyon Towhees has been reported to fly with the female as she carries nesting material (Johnson and Haight 1996; J. T. Marshall, pers. comm.). This was subsequently verified by extracting DNA from the feathers and ascertaining the young possessed the mtDNA of Abert's Towhee (R. M. Zink, pers. comm.) The pair frequently engaged in *squeal-duets* when greeting each other, a trait of both species (Marshall 1964).

The nest was 1.9 m above ground and measured 7.6 cm tall with 12 cm outside, and 7.6 cm inside diameters. The nest contained three eggs on 27 April and on 8 May the nest contained three nestlings, estimated to be 4–5 days of age. The nestlings weighed 18.2, 25.5, and 26.5 g on 11 May; the smallest did not have its eyes open. We banded all 3 nestlings.

We observed 22 provisioning trips to the nest on 12 May, 12 by the Abert's and 10 by the Canyon Towhee. The Canyon Towhee flew south into desertscrub during forays from the nest, while the Abert's Towhee flew north into the mesquite bosque for foraging. This difference in habitat preference by each adult was noted on numerous occasions.

The young fledged on 18 or 19 May, and the adults immediately moved them into a wooded

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region too thick for close observations. They led the fledglings back into open areas within ~1 week making them easier to observe. We observed parents feeding the young between 27 and 31 May. Particular young were generally favored by individual parents, suggesting brood splitting (Marshall and Johnson 1968, Johnson and Haight 1996). However, on two occasions we observed a single fledgling being fed by both parents. One fledgling was observed bathing in a birdbath on 30 May.

The female spent more time in the mesquite bosque during this period, and the male was more attentive to the young, leading us to suspect the pair was engaged in building a second nest. We observed the pair copulating on 29 May with the *P. fuscus* in the superior position.

The *P. fuscus* adult was observed alone in mid-June with one of the banded fledglings. The central breast spot of the young bird was evident at this stage but the throat patch was less conspicuous than that of the adult. The adult and young engaged in *squeal-duet* vocalization when meeting, a behavioral trait previously unreported between adult and young "brown towhees." None of the banded young was observed following this initial post-fledgling period.

We discovered both adult towhees feeding unbanded fledglings in late August 1999 and recorded their appearance (Appendix). We later saw only the adult mixed pair as they frequently visited the bird-feeding area together throughout the winter months. The parents were observed feeding three fledglings on 15 May 2000. A Cooper's Hawk (*Accipter cooperii*) flew overhead as all five towhees fed on cracked corn in the open yard on 17 May. Both parents uttered a series of short, sharp, shrill *peet* or *pink* calls. These calls sounded identical in both parents and caused the fledglings to "freeze." The young were observed sporadically (and described, Appendix) over the next few weeks and the adults remained on territory, but were not seen after November 2000.

DISCUSSION

Intrageneric Hybridization.—Several factors are important regarding this Tucson "brown towhee" hybridization. These include: (1) hybridization has not been reported earlier between *P. aberti* and *P. fuscus* in the Tucson region, although studies of "brown towhees" have been conducted in this vicinity for more than 100 years (Bendire 1890; Marshall 1960, 1964; Marshall and Johnson 1968; Johnson and Haight 1996); (2) the pair bond between congeneric species that are not sisters (Zink 1988, Zink and Dittmann 1991) was sufficiently strong to last 2 years and allow raising of at least three broods; (3) the female *P. aberti* selected a male *P. fuscus* at a locality where other *P. aberti* are not uncommon; and (4) the problem of detecting hybrids is exacerbated by the fact the F_1 hybrids appeared so similar to *P. fuscus*. However, no interbreeding was found among several hundred color-banded birds in a multi-year study in an environment inhabited by both species, near Tucson, Arizona (Marshall 1960, pers. comm.).

The residential yard near Tanque Verde Creek was in an ecotone which provided feeding sites. Both towhee species prefer feeding in open areas immediately adjacent to brush into which they may escape if disturbed (Marshall 1960, Dawson 1968, Marshall and Johnson 1968). Thus, the open yard between the brushy hillside and mesquite bosque provided an ideal situation for hybridization of *P. fuscus* and *P. aberti*.

A second mixed pair of "brown towhees" occupied a territory during 2007–2009 in the foothills of the Tucson Mountains ~12 km west of downtown Tucson (S. M. Russell, pers. comm.; RRJ, pers. obs.). The immediate surrounding landscape is a mixture of native upland Sonoran desertscrub with artificial plantings maintained by drip irrigation, forming habitat more mesic than native Sonoran desertscrub. This pair, similar to the Tanque Verde mixed pair, was first noted as they commonly appeared at and left a feeding station together. The pair would disappear into the adjacent desertscrub on leaving the feeding station. Male/female identity of this pair of *P. fuscus* and *P. aberti* remain unknown along with their breeding history. The pair built a nest in 2008 that failed to fledge young (S. M. Russell, pers. comm.). However, Russell noted an immature "brown towhee" during the 2009 breeding season that he judged to have at least some *P. aberti* characteristics, e.g., black markings on the face. Russell noted only the single mixed towhee pair in the yard during this period with no pairs of either *P. aberti* or *P. fuscus*. During October and November Russell noted two *P. aberti* (presumably a pair) in this yard but no *P. fuscus*.

Habitats are newly created through landscape disturbance that provide new niches. Processes are telescoped in time in human-disturbed habitats, compared to natural processes such as ecological succession. Both sets of mixed *P. aberti* and *P. fuscus* pairs in our study were in irrigated residential

yards. Disturbed habitat has had a profound influence on avian hybridization on the Great Plains in numerous passerine species. The entire Great Plains may now be considered a large hybrid zone between several related eastern and western species that nest in woody vegetation (Gill 1998).

Shifting Habitat Selection by Abert's Towhee.— A shift in habitat selection and local distribution by *P. aberti* has occurred recently in Tucson when arid desertscrub ecosystems were replaced by relatively mesic irrigated yards and parks. *P. aberti* was not listed as a resident of housing developments in Tucson's suburban uplands in studies as recently as the 1980s (Tweit and Tweit 1986, Mills et al. 1989). *P. aberti* has now been recorded in suburban yards as far as 7 km from its original riparian habitat along the Santa Cruz River, increasingly encroaching on areas that had been occupied by *P. fuscus* (Tucson Audubon Society 2001–2009; RRJ, pers. obs.). These changes have increased the probability of *P. aberti* and *P. fuscus* occurring together and the possibility of hybridization. Whether *P. aberti* will displace *P. fuscus* in much of suburban Tucson or the two species will coexist is unknown.

A similar movement occurred by *P. aberti* in the Phoenix region during the 1900s. The species moved from the now dry Salt and Gila rivers into suburban yards and agricultural areas (Johnson et al. 1987, Rosenberg et al. 1987). However, in Phoenix, *P. aberti* does not come into contact with *P. fuscus*, which occurs only in more remote arid upland areas (Rea 1983, Johnson et al 1987).

It is probable that disturbed native habitat in the Tucson area, as well as ecotonal factors, facilitated the Tanque Verde towhee hybridization and Tucson Mountain mixed pairing. It is possible that hybridization is a recent phenomenon caused by newly created habitats stemming from human landscape alteration. It is also possible the difficulty in distinguishing hybrid offspring has led to an underestimation of the frequency of hybridization. Thus, a search should be undertaken in avian collections for hybrid towhees.

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APPENDIX.—Characteristics of eight young F_1 hybrids in three broods from *Pipilo aberti* × *P. fuscus* cross. Colors and characteristics were ascertained through field and photographic comparisons with the parents, by examination of specimens in the University of Arizona bird collection, and from *Birds of North America* accounts (Tweit and Finch 1994, Johnson and Haight 1996). All characteristics are most like *P. fuscus* unless otherwise noted.

General body color of all eight was intermediate between that of the two parents but most other characteristics were similar to adult *P. fuscus*. All showed throat patches varying from light to darker and striping around the patch varied from much to none. No young had the dark facial mask or uniform pinkish-brown of breast, flanks, and belly of female *P. aberti*. The only obvious *P. aberti* characteristic for any of the young was the dark rusty crissum (under-tail coverts) of five F_1 hybrids, in contrast to the lighter, buffy crissum of *P. fuscus*. Photographs available by using the second author's complete name in a search engine or at http://zeeman.ehc.edu/envs/Hopp/index.html.

Brood # 1 (May 1999; 3 F_1 Hybrids

Two with hint of rufous crown; third with uniform gray-brown crown. All with central breast spot. Two with more extensive, bright, rusty crissum, most like *P. aberti*.

Brood # 2 (August 1999; 2 F_1 Hybrids)

Both with slight but detectable rufous crown. Throat patch for both notably darker and less pronounced than in adult *P. fuscus*. One with slight breast spot. Tails of both longer than adult *P. fuscus*. Both with more extensive, bright rusty crissum, most like *P. aberti*.

Brood # 3 (May 2000; 3 F_1 Hybrids)

One with evident and two with slight rufous crown. One with central breast spot smaller and less conspicuous than adult *P. fuscus*, second with heavy streaking approaching a spot, and third without a spot. Tails of both similar in length to adult *P. fuscus*, slightly shorter than *P. aberti*. Bright rusty crissum in one, less evident in second, and third with no color difference between belly and crissum, appearing similar to front view of female Brown-headed Cowbird (*Molothrus ater*).

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Yellow-billed Cuckoo Hatched and Fed by a Red-winged Blackbird

Ken Yasukawa[1]

ABSTRACT.—I observed a Red-winged Blackbird (*Agelaius phoeniceus*) nest in southcentral Wisconsin, USA that received a Yellow-billed Cuckoo (*Coccyzus americanus*) egg. The cuckoo egg was laid after the blackbird clutch was complete and the female had begun incubation. The parasitic egg was considerably different in size and color, but was accepted by the female Red-winged Blackbird. The female, but not the male, also cared for the nestling, which was strikingly different in plumage, gape markings, and begging behavior, and which grew despite its 3–4 day hatching delay relative to its nest mates. Rapid development and exaggerated begging behavior of the Yellow-billed Cuckoo nestling may enable a parasitic cuckoo nestling to compete successfully with host nestlings for food. *Received 24 August 2009. Accepted 11 December 2009.*

Yellow-billed (*Coccyzus americanus*) and Black-billed (*C. erythropthalmus*) cuckoos are the only altricial birds that lay in the nests of other birds as apparent facultative, as opposed to obligate, interspecific brood parasites (Hughes 1999). Wyllie (1981) noted intraspecific parasitism also occurs,

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FIG. 1. Nestling Yellow-billed Cuckoo (right) begging in a brood of Red-winged Blackbirds.

and Fleischer et al. (1985) used egg protein analysis to verify that two female Yellow-billed Cuckoos contributed to a large clutch. The majority of records of interspecific parasitism are between Yellow-billed and Black-billed cuckoos (Nolan and Thompson 1975), but 11 other species are known to have been parasitized by Yellow-billed Cuckoos. Many of the unusual aspects of North American cuckoo reproductive ecology, including the tendency to vary clutch size in relation to food supply and rapid nestling development, may have facilitated evolution of brood parasitism in cuckoos (Nolan and Thompson 1975). I report an unusual case of brood parasitism of a Red-winged Blackbird (*Agelaius phoeniceus*) by a Yellow-billed Cuckoo and discuss an aspect of cuckoo nestling behavior that may have facilitated the evolution of parasitism.

OBSERVATIONS

On 21 May 2009 I found a Red-winged Blackbird nest containing four incubated eggs at Newark Road Prairie in southcentral Rock County, Wisconsin (42° 32′ N, 89° 08′ W). I checked this nest daily at ~ 0530 hrs CST. On 24 May I found an egg of a Yellow-billed Cuckoo in addition to the four blackbird eggs. The cuckoo egg was considerably larger than the blackbird eggs (Hughes [1999] gives a mean egg mass of 9.1 g for eastern populations of Yellow-billed Cuckoos, whereas Yasukawa and Searcy [1995] give mean masses of 4.02–4.07 g for Red-winged Blackbirds). The egg was pale bluish-green and unmarked, unlike the blackbird eggs, which were pale blue with dark brown blotches. All five eggs were warm to the touch, indicating the female was incubating them. On 28 May I observed one newly hatched blackbird nestling and by the next morning, there were three blackbird nestlings along with one blackbird egg and the cuckoo egg. When I checked the nest on the morning of 1 June, the Yellow-billed Cuckoo egg had hatched. The cuckoo nestling was thus 4 days younger than the first-hatched blackbird nestling and 3 days younger than the other two blackbird nestlings. The fourth blackbird egg did not hatch and showed no signs of development when I examined its contents on the morning of 3 June.

The Yellow-billed Cuckoo nestling was strikingly distinct from the Red-winged Blackbird nestlings in appearance (Fig. 1) and behavior. Unlike its blackbird nest mates, when begging the cuckoo nestling rapidly vibrated its head, produced a sustained hissing begging call while showing its distinctive gape with white spots, flapped its wings rapidly, and attempted to gain a position above the blackbird nestlings by standing

on them. In contrast, the blackbird nestlings moved their heads only slightly as they stretched their necks and gaped. The blackbird gape lacked the white spots of the cuckoo, and the blackbird nestlings did not flap their wings or jostle for position. The blackbird begging call was a series of discrete chirps rather than a sustained hiss. I made a 1-hr video recording of the nestlings on 4 June to document the differences in nestling begging behavior between the two species. Unfortunately, a predator, probably a common raccoon (*Procyon lotor*), took the nestlings that night, and I could not continue my observations of this unusual case of brood parasitism to learn whether the fledgling would have received care.

DISCUSSION

Unusual reproductive behavior in Yellow-billed Cuckoos is associated with abnormal food abundance (Nolan and Thompson 1975) but, to the best of my knowledge, 2009 was not an outbreak year for eastern tent caterpillars (*Malacosoma americana*) or periodic cicadas (*Magicicada* spp.), and the numbers of annual cicadas (*Tibicen* spp.) did not seem unusual. The most recent outbreak of periodic cicadas in Rock County, Wisconsin was 2007 (Hamilton 2007).

The egg and nestling of the Yellow-billed Cuckoo were quite different from those of the host Red-winged Blackbird, but the egg was accepted (incubated) and the female blackbird fed the nestling. I did not observe the male blackbird feeding nestlings. Nickell (1954) reported a similar case in Oakland County, Michigan. Furthermore, the 3–4 day difference in hatching did not appear to disadvantage the cuckoo nestling, whereas a blackbird nestling experiencing the same hatching asynchrony would normally die of starvation (Holcomb and Twiest 1971, Strehl 1978).

Red-winged Blackbirds accept Brown-headed Cowbird (*Molothrus ater*) eggs and care for cowbird nestlings and fledglings, and Brown-headed Cowbird parasitism is common on my study area (Clotfelter and Yasukawa 1999). Yellow-billed Cuckoos are observed on my study area in most breeding seasons as well, although they are not common. Given the number of studies of Red-winged Blackbird reproductive biology, extensive overlap in Red-winged Blackbird and Yellow-billed Cuckoo breeding ranges, and dearth of similar records in the literature, Yellow-billed Cuckoo parasitism of Red-winged Blackbirds is clearly rare.

Nolan and Thompson (1975) suggested that North American cuckoos have traits that facilitate the evolution of brood parasitism (see also Hughes 1999). These traits include nomadic movements in response to food abundance, large egg size, variable clutch size in response to food availability, intraspecific brood parasitism, occasional use of abandoned nests of other species, short breeding cycle (17 days from egg laying to fledging is among the shortest of any species of bird), rapid nestling development (nestlings can raise their heads above the nest rim and are fully feathered within 2 hrs after hatching), extreme hatching asynchrony, and an unusual diet of food items that can be difficult to find. Yellow-billed Cuckoos occasionally lay eggs in nests of other species (called "incipient parasitism" by Nolan and Thompson 1975), and a necessary behavior is in place to allow evolution of brood parasitism if parasitism was to become more advantageous than parental care (Hamilton and Orians 1967). North American cuckoos have not evolved obligate brood parasitism, however, perhaps because species recognition, song learning, and ecological constraints act to maintain the advantage of parental behavior.

Acceptance of a Yellow-billed Cuckoo egg and nestling by a Red-winged Blackbird may be another indication of the plastic nature of parental care in North American songbirds (Shy 1982). However, the exaggerated begging behavior of the nestling and its ability to overcome hatching 3–4-days later may indicate they facilitated the Yellow-billed Cuckoo's ability to secure food from the female Red-winged Blackbird despite the obvious differences in plumages, begging calls, and begging behavior of the two species. The ability to compete for food in novel and/or more exaggerated manners than host nestlings would also facilitate the evolution of obligate brood parasitism.

ACKNOWLEDGMENTS

I dedicate this short communication to my mentor, Val Nolan Jr. I thank C. S. Anderson for field assistance and Beloit College for permission to work at Newark Road Prairie and financial support. S. G. Sealy and J. M. Hughes provided background information on North American cuckoo parasitism, and E. D. Ketterson, E. D. Clotfelter, and two anonymous reviewers made suggestions to improve earlier versions of the manuscript.

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Ornithological Literature

Robert B. Payne, Review Editor

FIELD GUIDE TO THE SONGBIRDS OF SOUTH AMERICA: THE PASSERINES. By Robert S. Ridgely and Guy Tudor. University of Texas Press, Austin, Texas, USA. 2009: 750 pages and 122 color plates with facing-page maps. ISBN: 978-0-292-71979-8. $49.95 (paper).—There is much to celebrate with publication of this revamp and update of the first two volumes of *The Birds of South America* (*BOSA*: Oscine passerines, 1989; Suboscine passerines 1994) in a more compact format under a single cover. Undoubtedly the most anxiously awaited aspect of *Songbirds* is the tremendous contribution of Guy Tudor's new art; illustrations of 406 species (some as only busts) have been added to the ~1,220 previously depicted ones, a whopping 33% increase. There remain not illustrated about 347 native species of South American passerines, roughly 18% of the authors' total number of ~1,974 (excluding a few vagrants). Now represented are all but one (I think) standing genus (*Stymphalornis* antbirds, endemic to southeast Brazil).

The back cover calls attention to the need for "a more compact guide that birders can take into the field." Given that they intend to show us how to identify 1,981 species of passerine birds, some of which are hard to see well, all while traipsing through the rainforests and deserts on the Bird Continent, they may have set themselves up for disappointment. On some levels, they have succeeded, it's just hard to say whether they have tackled the monster or the monster has tackled them. Weighing in at 1.28 kg, the book *can* be carried in the field by most birders, but not very comfortably by anyone. Perhaps most tellingly, almost no one has opted to tote it on recent South American birding walks where most folks would like to be carrying a field guide. I've not yet seen anyone with the plates cut out and bound separately, all too often the fate of *BOSA*, but the specter has already come up. The ideal bulk may lie about halfway between *Songbirds* and the much smaller *Birds of South America: Nonpasserines* (Erize et al. 2006, Princeton University Press).

Tudor's illustrations are wonderful; it's hard to imagine ever seeing paintings of many of these birds that are more "spot-on." In large measure because he is an avid and highly observant birder who understands the importance of accurate shapes and postures, Tudor is able to encapsulate what we need for *field identification* in the strict confines of a *field guide*. As is inevitably the case when a large number of species is treated, a few illustrations leave much to be desired (most of which are holdovers from *BOSA*). White-bearded Antshrike (*Biatas nigropectus*, Plate 20, #3) never appears uncrested (except in a museum tray)—the new, undersized male figure and a female bust, at appropriate scale, could have admirably replaced the poor *BOSA* ones; Plain-crested Elaenia (*Elaenia cristata*, Plate 44, #7), unrecognizable as is, shows a sharp, spiky crest virtually all the time; White-winged Cotinga (*Xipholena atropurpurea*, Plate 69, #7) is a much darker "blackish-purple" as described in the text; Black-collared Swallow (*Atticora melanoleuca*, Plate 76, #10) invariably looks black-and-white (not navy blue) in the field even at close range, and the posture is atypical; and all of the pipits (*Anthus* spp., Plate 84, perhaps with the exception of Correndera Pipit, *A. correndera*) remain unidentifiable in and of themselves.

Other closely similar groups of birds, such as the dreaded "tyrannulets," are well done although there are regrettable problems with a few species that occur in syntopy (together in the same habitat) through much of their ranges, particularly Rough-legged Tyrannulet (*Phyllomyias burmeisteri*, Plate 41, #16); Greenish Tyrannulet (*P. virescens*, Plate 41, #17); and Mottle-cheeked Tyrannulet (*Phylloscartes ventralis*, Plate 46, #4). The most similar-looking small tyrannids, scattered over several plates (mostly 41, 42, 46), could have been grouped in a much more useful manner for field identification, for starters by separating exclusively Andean from non-Andean species on different plates, then bunching the members of each broad group that actually overlap geographically and occur in the same habitats. Because the small South American tyrannids, too many of which are not illustrated, present the most complex field identification

problems (female *Sporophila* seedeaters aside), I had hoped they would be given high priority in *Songbirds*.

The choice was made to insert many of the new illustrations at varying scales different from the rest of the (existing) figures on the plate. Some of the most problematic instances are Plate 52, #8, 11; Plate 53, #3, 4, 11, 13 relative to the themselves and the rest of that plate; Plate 61, #5, 7; Plate 71, #4; Plate 101, #2, 3; and Plate 114, #12 (Dickcissel [*Spiza americana*] should be significantly larger than Greenish Yellowfinch [*Sicalis olivascens*]!). It is disheartening to see the stunning Araripe Manakin (*Antilophia bokermanni*, Plate 64, #17) relegated to a corner-squeeze at about half-size, below its sister, Helmeted Manakin (*A. galeata*). Its illustration points to another unfortunate feature of all plates having new illustrations: something happened in the production stage so all of the new figures look faded relative to those in *BOSA*. Thus, the red and black on the Araripe Manakin are significantly paler or less saturated than these same colors on the Helmeted Manakin. A number of figures of females also have been newly illustrated, an important advancement, but a field guide really must treat all distinctive female plumages (of the species illustrated at all). Almost no juvenal plumages are shown or described. One of the few, Andean Laniisoma (*Laniisoma buckleyi*, Plate 66, #8), is mislabeled the adult female. I love the new illustrations of the mockingbirds (Plate 83) in flight; it would have been great to see much more of this kind of field-oriented illustration.

On the plates, each species illustration is numbered and some also have letters A, B, C, indicating the figure represents a distinctive subspecies. To interpret this information, one needs to go to the text. This cumbersome system could have been made much less so by simply putting the letters on the species' map to inform users of where that taxon (or group of taxa) is expected.

The South American distribution of each species is shown on a correspondingly numbered map on pages opposite or near its illustration, sometimes requiring a little hunting although I got used to it. I really like these maps. Several levels of geographic zoom are used to show most of the highly restricted ranges more clearly. The contrast between colors chosen for ranges, including migrants, and also rivers and political boundaries for most countries (to the state/department level in the tightest zooms), also works well. Without having looked at most of the maps critically, I think it's fair to say the level of accuracy is admirably high. I happened to notice that the maps for Black Antbird (*Cercomacra serva*) and Blackish Antbird (*C. nigrescens*) were switched (their names are bad enough!). Similarly, numbers labeling the maps and figures for Green Honeycreeper (*Chlorophanes spiza*) and Red-legged Honeycreeper (*Cyanerpes caeruleus*) are mixed up (numbers are correct on the maps and text, so switch the species' numbers *on the plate* of your copy to match). Problems on the level of not showing Saffron-crested Tyrant-Manakin (*Neopelma chrysocephalum*) in northern Peru; of showing Long-winged Antwren (*Myrmotherula longipennis*) extensively between the Rio Napo in Peru and the Negro in Brazil where it is largely or completely absent; of missing the interface between Squamate Antbird (*Myrmeciza squamosa*, shown extensively north into Rio de Janeiro) and White-bibbed Antbird (*M. loricata*, shown far too extensively through interior Bahia, and ranging well into northern coastal São Paulo); of White-breasted Antbird (*Rhegmatorhina hoffmannsi*) crossing (and extensively so) the Rio Juruena into northern Mato Grosso; of Serra do Mar Tyrannulet (*Phylloscartes difficilis*) occurring all along the coast of southeast Brazil where known from only a few scattered points high in the mountains; and of showing the threatened Black-and-white Monjita (*Xolmis dominicanus*) over much too wide an area in Rio Grande do Sul (it was never known to be so amply distributed, even historically)—are somewhat more frequent. Maps for a few very poorly known birds are annoyingly problematic. For example, an undocumented, single-observer sight-record of the ultrarare Kinglet Calyptura (*Calyptura cristata*, Plate 66, #6) in coastal northern São Paulo is mapped and cited in the text as if it were fact! This map should show only the single point of known occurrence (from late Oct 1996) just below Teresópolis, Rio de Janeiro with an arrow pointing to a red dot and at most a question mark anywhere else; the maximum zoom should have been provided here.

In a field guide, the species accounts should foster transformation of the painting on the plate to a living bird by infusing vital information on habitat and behavior while enabling even the most difficult field identifications. My overall impres-

sion is that over 90% of the species accounts in *Songbirds* are good to excellent; space limitations in the Journal precluded my elaboration of examples. Transcriptions of vocalizations of most species are offered, which is usually better than not having anything but not nearly as helpful as actually hearing the sounds. I highly recommend obtaining recordings (primary vocalizations of most species have been published or are available on the internet) ahead of travel to South America.

The taxonomy used in *Songbirds* closely parallels that of the standing South American Checklist Committee (SACC) of the American Ornithologists' Union. The SACC was obviously heavily referenced although it was not cited anywhere in a 16-page section toward the back of the book titled "Notes on Taxonomy and English Names." However, the authors "expressly note" (page 2) that they "adhere to the decisions on English names and taxonomy" that were recently published on behalf of the International Ornithological Congress (IOC; Gill et al. 2006–2009, *Birds of the World, Recommended English Names*, Princeton University Press). The first bird in the book, Campo Miner (*Geositta poeciloptera*), provides a poignant example of the taxonomic swirl that underlies *Songbirds*. It boils down to: (1) the IOC classification, which incorporated new information up to the end of 2004, maintaining the long-standing *Geobates* contrary to a 2003 publication suggesting it be merged into *Geositta*; (2) the SACC invoking primarily genetic data published in 2005 to merge *Geobates* into *Geositta*; and finally (3) *Songbirds* incontrovertibly following the SACC, not the IOC.

Ornithologists and birders frequently express their opinions that some taxa or populations of birds could or should be considered distinctive enough to merit species status. The unilateral splitting or lumping of species by authors of such works as *Songbirds* and other guide books in which no data or analyses of the case(s) are presented for peer-review or independent evaluation (now or a hundred years from now) reside in a bubble drifting around the perimeter of science, a "gray" subspecies of taxonomy. In *Songbirds*, Ridgely and Tudor are "gray" on ~25 taxa traditionally considered subspecies. All are interesting cases worthy of focused study, and the SACC and other taxonomic committees will soon consider not only all of them but also all of the equally or more interesting cases that, for one reason or another (we have no data to judge), were not mentioned in *Songbirds*. For one example, the *Stigmatura* wagtail-tyrants go from two to four species absent any analysis at all but the well-supported (and accepted by the SACC) elevation to species status of *Schistocichla leucostigma saturata* (Roraiman Antbird, in the Spot-winged Antbird complex) published in 2005 was not recognized.

English names are not bound by scientific principles, and their usage for South American birds became particularly unstable after the mid-1980s, when *BOSA* introduced changes to names of long standing. In *Songbirds*, the 2006 IOC classification is followed, even in cases where a novel name of Ridgely's from *BOSA* (e.g., Noble Antthrush for *Chamaeza nobilis*) was rejected in favor of the traditional name (Striated Antthrush). But this has set up some conflicts. For example, a nomenclatural note on page 691 reads, "We rename *Mitrephanes phaeocercus* the Northern (rather than the Common) Tufted Flycatcher, preferring to restrict the use of the name "Common" to species that truly are so." This flycatcher was described from Mexico and most of its range lies in Middle America. Ridgely and Gwynne (1989, *A Guide to the Birds of Panama*, Princeton University Press) introduced the modifier "Common," and described its status in Panama as "Common." Pointless self-reversal like this does not inspire confidence and promotes instability of names. True to form, Ridgely has not resisted unveiling a few English names that almost seem designed to shake things up. My vote for the standout is ... "Shrike-like Tanager" (in place of the entrenched White-banded Tanager, *Neothraupis fasciata*), not to be confused with *Lanio* Shrike-Tanagers. In sum, there is a great deal of arbitrariness displayed throughout the taxonomy and English naming used in *Songbirds*.

The new Ridgely and Tudor *Field Guide to the Songbirds of South America* should become a standard in the libraries of all birders, ornithologists, and conservationists interested in neotropical birds, and it is sure to make birds more accessible to more people, which is at the grassroots level of effective bird conservation. If you ever dream of birding in South America, buy and thoroughly enjoy this book. Take it to South America with you and use it to ably identify the vast majority of passerine birds you will see.—BRET WHITNEY, Louisiana State University Museum of Natural Science, 119 Foster

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PALEOGENE BIRDS. By Gerald Mayr. Springer-Verlag, Berlin Heidelberg, Germany. 2009: 262 pages and 64 figures. ISBN: 978-3-540-89627-2 ($189.00 USD, cloth; ~$25 per chapter in electronic form).—The Paleogene Period, from ~65 to 23 million years ago, witnessed profound shifts in the earth system including the origin of permanent ice sheets in Antarctica. Global cooling from peak "greenhouse Earth" conditions is linked to a retreat of Eocene paratropical forests previously extending to the poles and the development of the "icehouse" conditions of the present. Across the same time period, shifts in the ecology, diversity, and distribution of nearly every part of the biota are inferred. New insights into every part of these Paleogene shifts have been rapidly accruing in recent years. The record of sea-surface temperatures and global climates has been significantly refined, and vertebrate paleontologists continue to further inform our knowledge of changing faunas.

The rapid pace of new discoveries of fossil bird species in recent years belies the general idea of their impossibly fragmentary record. The early history of extant crown clade avian diversity, species of which are parts of the major bird lineages alive today, has been partially tracked in several short review articles eager to summarize the rush of new data recovered in recent years. Because relevant paleo-ornithological discoveries are moving forward at an arguably unprecedented pace, any summaries must be proximate, abbreviate, and soon out of date. However, the last book-length review focusing on an overlapping time period and set of taxa is the 1999 Second Edition of A. Feduccia's "*The Origin and Evolution of Birds*" (Yale University Press). With a few exceptions, including updating several chapters presenting the author's views on the dinosaurian affinities of birds, most of its content is from the 1996 First Edition. It is into this context that Gerald Mayr, Curator of Ornithology at the Senckenberg Institute, offers a significant contribution, a detailed new guide to fossil avian diversity from the first part of the Cenozoic. In ~250 dense small-format pages, "*Paleogene Birds*" neatly presents insights into ~40 million years of the early evolution of extant bird lineages. The book is largely organized taxonomically but also includes a brief overview of principal fossil localities, a review of debates concerning the relationships among major clades, and conclusions regarding the historical patterns of avian diversity in the Northern and Southern hemispheres.

Mayr, who recognizes in his preface that any review in the present intellectual context will quickly need updating as new discoveries are made, quite thoroughly summarizes the earlier literature but focuses on key recent discoveries, a great many of which he has made. The community would profit from this book even if it were merely a synthesis of Mayr's own work. A prolific author, he has published over 150 papers since 1995, more than any other paleo-ornithologist over the same time period.

Ornithologists of all kinds will be intrigued by the bizarre turns that avian evolution took in the first part of the Cenozoic. The book presents exceptional fossils that record novel ecologies and distributions for well known groups: e.g., Old World hummingbird relatives, giant flightless divers, and sea birds with bony pseudoteeth. However, at ~$189 USD for a new copy of this slim volume, many non-specialists may elect to visit their local libraries or hope for a lower-price soft cover edition. The intended primary readership of the book is the paleo-ornithological community. However, it will also serve as an important reference for other ornithologists and paleontologists seeking access to specific parts of the literature. The book seems organized for, and best approached by, skipping from section to section, rather than reading from cover to cover. Illustration print quality is excellent, although the specialist might wish for an oversized volume with color illustrations and larger photographs.

One is well served by the detailed presentation of Mayr's perspective as that perspective is often thought-provoking. Much of the data presented is fascinating, and comments made as small asides could be expanded into journal articles of considerable interest. Some of the more controversial ideas forwarded by Mayr and summarized in the book concern phylogenetic relationships among major lineages of birds; e.g., regarding the affinities of penguins with parts of former "Pelecaniformes." While not all readers will agree with these hypotheses, all are supported by clearly presented evidence that is well positioned to inform new research questions.

We still have much to learn about patterns and

potential drivers of avian evolution. Mayr clearly stands with the rest of us in wondering what new bizarre forms we may discover tomorrow. It is striking how few avian taxa are generally shown in the skies of Paleogene ecosystem reconstructions. It is hard not to feel as if we have been missing significant patterns in vertebrate evolution across the Cenozoic greenhouse to icehouse transition. This book offers an important opportunity to renew our focus on the diversity and distributions of birds as significant parts of Paleogene environments.—JULIA A. CLARKE, Associate Professor, University of Texas, Department of Geological Sciences, 1 University Station C1100, Austin, TX 78712, USA; e-mail: Julia_Clarke@jsg.utexas.edu

BIRDS OF BORNEO. By Susan Myers. Princeton University Press, Princeton, New Jersey, USA. 2009: 272 pages, 1,592 color illustrations, 630 maps. ISBN: 978-0-691-14350-7. $29.95 (paper).—At last, ornithologists and birdwatchers in Borneo have a complete and accurate guide to birds that they can fit in their pockets. For 30 years, folks have worked to this end, and it is extremely gratifying to have reached it. Starting in the late 1970s, Bertram Smythies' magnificent handbook, *The Birds of Borneo* (1960, 1968), was out of print and the first modern field guide to the birds of southeast Asia (King et al. 1975) did not cover Borneo. Thus, there was a great need for a handy book on Bornean birds. The Sabah Society helped alleviate the problem by publishing an inexpensive version of Smythies (1981), but it was too big for field use. Charles Francis (1984) also helped by producing a pocket guide consisting of Smythies' plates, but the illustrations without text were not adequate for identification of many species. For the last 15 years, Bornean bird enthusiasts have done pretty well with MacKinnon and Phillipps (1993), the first field guide to birds of the Indo-Malayan Archipelago. It has excellent illustrations by Karen Phillipps, but is now out of print. Also, because it includes all the birds of Sumatra, Java, and Borneo, it is too big and bulky for comfortable use in the field. Because it was published before knowledge of Bornean bird distribution and ecology had quite gelled, it also contains lots of small mistakes.

Those problems are now history. The tremendous recent growth in sophisticated birdwatching in Borneo, combined with comprehensive updates in the scientific literature (Smythies 1999, Sheldon et al. 2001), set the stage for a good field guide. The guide's author, Susan Myers, has led Victor Emmanuel Nature Tours in eastern Asia for more than 15 years. Thus, she has been an integral part of the ecotourism phenomenon. She combines great experience in finding and identifying birds in Borneo with a grand perspective of Asian birds as a whole. The result of these congruent forces is a truly outstanding field guide. It is small, has extensive color illustrations of all the birds, a complete set of maps, and all the information needed on plumage, distribution, habitat, elevation, and behavior to sort out the species. It really is excellent.

The quality of any field guide depends on insightful, pithy descriptions, and high quality illustrations. This book does well in both areas. A good test of its description quality is how well the author deals with difficult groups. Such a group in Borneo is the *Cyornis* flycatchers. These blue and brown birds of the forest understory look much the same, have nondescript songs, and often confuse newcomers (Smythies resorted to a key to deal with them). Myers, with simple, skillful descriptions of plumage, similar species, microhabitats, and behavior makes it easy to sort them out. As for illustrations, each species is depicted individually next to its description and distribution map, instead of in plates of similar taxa. Sexually dimorphic plumages, age variants, and occasionally alternative subspecies are provided. Most of the figures have been reproduced individually from the plates in Robson (2000), but 295 (of 180 species) were prepared specifically for this book. This helps explain the large number of contributing artists (16) and the variation in illustration quality. Despite variation, only a couple of paintings are sub-par (e.g., Malaysian Rail-babbler [*Eupetes macrocerus*] and crows). All the illustrations are more than adequate for identification, and most are really good. I particularly liked the trogons, hornbills, bulbuls, babblers, and muscicapine flycatchers. My favorites are the wren-babblers.

By virtue of its simplicity and thoroughness, this is an outstanding field guide. I really cannot wait to take it into the forest and give it a field test. No doubt it will hold up well.—FREDERICK H. SHELDON, Louisiana State University Museum of Natural Science and Department of Biological Sciences, Baton Rouge, LA, 70803, USA; e-mail: fsheld@lsu.edu

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BIRDS AND BATS OF PALAU. By H. Douglas Pratt and Mandy T. Etpison. Mutual Publishing L.L.C., Honolulu, Hawaii, USA. 2008: 290 pages. ISBN: 978-1-56647-871-7. $29.95 (paper).—Palau lies at the western edge of Micronesia. As a result of its relative proximity to the rich avifaunas of Asia, the Philippines, and New Guinea, Palau sustains a larger set of both resident and migrant birds than any other Micronesian island group. Most of Palau also is blessed with a rugged, raised limestone topography that has stifled deforestation and human habitation. It's a great place for birdwatching.

When I visited Palau in 1995 and 1997, I carried two field guides. The first was the rather small *Field Guide to the Birds of Palau* by John Engbring (1988, Conservation Office, Koror, Palau), which covered mainly resident species. The second was the more comprehensive *A Field Guide to the Birds of Hawaii and the Tropical Pacific* by H. Douglas Pratt, P. L. Bruner, and D. G. Berrett (1987, Princeton University Press, Princeton, NJ), which covered all island groups in Micronesia and Polynesia. H. Douglas Pratt and Mandy T. Etpison now have produced a nice, up-to-date field guide for the birds (and bats) of Palau, whether resident or migrant. The text of this book has an informal style of writing, which may be good for some readers and not so good for others. There are no subheadings in the species accounts, and one must look through paragraphs of text to glean information on field marks, vocalizations, etc. The scattering of typos, unitalicized scientific names, grammatical errors, etc. is not enough to distract the average reader. The only maps are aerial photographs or satellite imagery; while attractive with their intense shades of blue and green, the lack of a clearly labeled, line-drawing map hinders one's understanding of Palauan geography.

The overall design of the book is lively and attractive. The species accounts feature magnificent photographs, mainly by Etpison. Because nearly all of the photographs are unlabeled, however, you must make your own judgment about the age and gender of the bird depicted (if those attributes are determinable), not to mention what it was doing and where the photograph was taken. The single color plate of endemic birds, painted by Pratt, is excellent although it is placed, without warning and essentially unreferenced, in the introductory material. The 19 species of scolopacid sandpipers depicted on pages 199 to 207 are erroneously placed in the plover family (Charadriidae).

Disagreement about common names of birds abounds in the tropical Pacific, so it is little surprise that some of these issues surface in *Birds and Bats of Palau*. For example, following the lead of F. Gill and M. Wright (2006, *Birds of the World: Recommended English Names*, Princeton University Press), Pratt and Etpison call *Sterna bergii* (page 224) the "Swift Tern" rather than the more conventional, non-apodid name Great Crested Tern. On pages 28 and 228–231, I congratulate the authors for not adopting Gill and Wright's name "Angel Tern" for *Gygis alba* (= *Gygis candida*), although they do use this simply heavenly name in the useful checklist of species on pages 278–282, which presents the distribution of each species on each major island.

I'm not a big fan of proposing new common names in field guides, even though this practice has become widespread in these days of oversplitting to increase perceived endemism. The account of the kingfisher *Todiramphus* (often placed in the genus *Halcyon*) *cinnamominus pelewensis* helps explain my reservations. Usually

known as the Micronesian Kingfisher with distinctive subspecies on Guam (*T. c. cinnamominus*), Palau (*T. c. pelewensis*), and Pohnpei (*T. c. reichenbachii*), Pratt and Etpison now call it the Rusty-capped Kingfisher and regard it as endemic to Palau at the species level, even though they list it as *T. c. pelewensis* in the species account, checklist, and index. Here I quote the first and last paragraphs of the species account (pages 88–90) as they lay out their thinking about this bird.

"In most previous books this bird has been called Micronesian Kingfisher because it was regarded as one of 3 subspecies that make up that species. However, HDP has accumulated evidence (see below) that shows that those 3 supposed subspecies could not possibly interbreed successfully and that there is really no such thing as the 'Micronesian Kingfisher.' Until the details are properly published, however, we continue to use the traditional taxonomy, but re-christen this endemic Palau soon-to-be species with a distinctive English name."

"Differences among the so-called 'Micronesian Kingfishers' include voice, adult and juvenile plumage coloration, and nesting habits. Those on Pohnpei are larger, and look very much like Rusty-caps as adults, but the juveniles resemble the strikingly different Guam kingfisher. In that one, the white parts of the Rusty-cap's plumage are a rich rusty chestnut, and, unlike the other 2, adult females are distinctive with a white belly, but juveniles are like adults. These visual differences are what scientists call an 'isolating mechanism.' This is any behavioral, ecological, or physical characteristic that prevents two species from interbreeding, during the mating process or after pairs have formed. For example, Pohnpei kingfishers nest in cavities in termite nests, while the Rusty-capped uses tree cavities, since the termite nests in Palau are used by Collared Kingfishers. So even if, hypothetically, a Pohnpei bird and Rusty-cap would mate, they would not be able to decide where to nest! And we suspect that the 3 Micronesian forms might not recognize each other visually either."

Aside from the pitfalls of trying to mix popular writing with supposedly scholarly thinking, and issues of biological versus phylogenetic species concepts, they mention nothing about whether there is molecular evidence for differentiation among these kingfishers. Changes in nomenclature are compromised until they are properly documented in a peer-reviewed publication.

In the drawings that show the external parts of birds on page 29, the bill is divided into the "upper mandible" (= culmen or rostrum) and "lower mandible" (= mandible). For decades, ornithologists have puzzled other vertebrate biologists by using the word "mandible" (= lower jaw) in describing the upper part of the bill. Also on page 29, the tarsal joint (ankle) is called the knee, which of course is actually one joint higher, where the femur joins the tibiotarsus and fibula. Similarly, they incorrectly use "ankle" for the joint were the toes articulate with the metatarsals.

In spite of my criticisms, nobody interested in birds should visit Palau without this fine book. I wish that it had been available during my two trips there, and I hope that it becomes widely used by residents and visitors to this fascinating island group.—DAVID W. STEADMAN, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA; e-mail: dws@flmnh.ufl.edu

THE ECOLOGY AND CONSERVATION OF ASIAN HORNBILLS: FARMERS OF THE FOREST. By Margaret F. Kinnaird and Timothy G. O'Brien. University of Chicago Press, Chicago, Illinois, USA, and London, UK. 2007: 315 pages, 8 pages of color photos, numerous figures throughout. ISBN: 978-0-226-43712-5. $45.00 (cloth).—Hornbills are easily the most conspicuous of Asian forest birds. Their huge size and massive, sculptured bills project a striking image that is advertised by the hornbill's loud, demanding voice and whooshing wing beats. Dedicated fruit-eaters, hornbills have a dominant role in the seed-dispersal of trees and other plants. Sadly, both their large size and food habits predispose them to extirpation by hunting and forest loss, and hornbills are among the most threatened of Asian birds.

This book offers an impressive compilation of field research and literature review on the evolution, ecology, and conservation of these wonderful birds. Hornbills, despite their boisterous nature, are for the most part hard to get to know. Imagine the challenges of studying a bird that spends its life out of reach high in the forest canopy, that roams over vast areas of forest tracking hundreds of species of fruits, and that nests deep within the tree-hollow of a forest giant. A few teams of researchers have met these

challenges over the past three decades, Kinnaird and O'Brien foremost among them and, as a result, the mysteries of the complex life of the rainforest hornbills are revealed in this book.

The authors begin with two chapters that introduce the hornbills, their phylogeny and biogeography. I was surprised to learn the radiation of 31 species and nine genera of Asian hornbills, primarily rainforest dwellers, is believed to have been derived from savannah and woodland inhabiting African hornbills. Speciation within the geographically complex southeastern Asian land mass and myriad islands has created a hot-spot of hornbill diversity centered on the Malaysian Peninsula and the islands of Sumatra, Borneo, and Java, all once connected. Several unique features of hornbills are also discussed. Naturally, this includes a section on "Casque form and function" that weighs the evidence for the horny casque's role in social signaling (species recognition, sex, and age), structural support for the long bill, and as a battering ram in one amazing species, the Helmeted Hornbill (*Rhinoplax vigil*), the males of which engage in aerial jousting with head-on collisions!

The next two chapters characterize the forest habitat and diet of these hornbills. Habitats range from highly seasonal deciduous subtropical forests to evergreen tropical forests with only the most subtle seasonal variation. An important climatic influence is the occurrence once every few years of an El Nino Southern Oscillation drought that causes the synchronized fruiting of many species of trees which, at other times, withhold bearing fruit. This boom-or-bust food availability affects which years hornbills nest. Although capable and eager to hunt small vertebrates and insects with that deadly bill, forest hornbills achieve at best a dismal success rate and instead must rely on fruits to fill their dietary requirements. Dietary studies document 497 species of fruits consumed, with oily fruits favored. With some success, the authors tackle the seemingly impossible task of characterizing the temporal and spatial availability of fruit and how that availability affects hornbill abundance, community structure, and reproduction.

Once they've established an ecological context for forest hornbills, the authors delve into a range of topics on hornbill reproduction and social systems, specifically monogamy, territoriality, and cooperative breeding. It's worth highlighting one topic. A behavior for which hornbills are famous is that the female seals herself into the nesting cavity during incubation and nestling care. The brick-hard seal is made from a mortar of regurgitated fruit, feces, and other materials delivered by her mate and pasted to the rim of cavity entrance. Apart from fortifying the nest against predators, the seal could serve other functions, such as creating a more suitable microclimate within the nest. However, the authors argue for a social explanation, that the female is forcing the male to be the sole provider for the family.

Much of the field research on hornbills has focused on the evolutionary and ecological function of hornbills in seed dispersal–their role as farmers of the forest, as the book's title suggests. The authors exhaustively review this research and then attempt to model populations of hornbills, not just for the sake of the hornbills (minimal viable populations) but for the forest they serve (ecological functional populations). This topic leads into the final chapters on the threats to hornbill survival and the outlook for the future. And threats there are aplenty. Asian hornbills and the forests that support them are in a disastrous situation through large-scale deforestation and hunting driven by a dense and growing human population. The rate of forest loss in places like Sumatra is mind-boggling and depressing to any sensibility for biodiversity and wilderness. The authors map out a full range of realistic options for the conservation of hornbills and their forests, including parks and protected area, grassroots activities, and species management.

I was impressed by how much published research there is on hornbills, given the difficulty in studying canopy birds in tropical forests and the modest effort worldwide devoted to this field. I was also impressed by the command that Kinnaird and O'Brien have of their subject material. Throughout the book, the authors take care to bring together available data on each subject and to explore it in depth. The text is laden with numerical summaries and statistical tests that greatly bolster their explanations. This quantitative approach is enhanced by numerous tables and figures. The data are nevertheless limited, and the authors over-reach in their interpretation in places, such as dismissing for lack of evidence the role of predation in the evolution of nest-sealing (see review by M. Whitmer, 2008, *Auk* 125: 996–997). Kinnaird and O'Brien are certainly entitled to their views by the wealth of

information assembled here, but it may take decades more research by other scientists before some of these ideas are sorted out. There are eight pages of color photographs of hornbills by Tim Laman. The text is written in an easily read narrative style, although it is information-packed and therefore rather slow going. I didn't notice any errors. This book will be a classic on hornbill biology, and on the ecology and evolution of a group of fruit-eating and seed-dispersing birds.—THANE K. PRATT, P. O. Box 420, Volcano, HI 96785, USA; e-mail: thane-linda@earthlink.net

THE SECOND ATLAS OF BREEDING BIRDS IN NEW YORK STATE. Edited by Kevin J. McGowan and Kimberley Corwin. Cornell University Press, Ithaca, New York, USA, 2008: 712 pages, 25 two-page color paintings, 245 halftone drawings, 164 charts and graphs, and 512 color maps. ISBN: 978-0-8014-4716-7. $59.95 (cloth).—This important work is the result of the first statewide re-survey of the distribution of breeding birds. The first survey, *The Atlas of Breeding Birds of New York State*, edited by Robert F. Andrie and Janet R. Carroll (1988), summarized the survey data collected between 1980 and 1985. For the *Second Atlas*, 1,207 volunteers surveyed essentially the same 5,279 blocks from 2000 to 2005, exactly 20 years later, compiling over half a million records representing 248 species and three hybrids. The result is an invaluable record, not only of the current distribution of breeding bird populations, but also the change in distribution over the past two decades. Change is occurring at a surprising rate; the *Second Atlas* documents changes, both increases and decreases, experienced by more than half of the state's species.

The book opens with six introductory chapters. In the first, Kimberley Corwin introduces the project and the methodology. As in the original atlas, the spatial units were based on 10-km × 10-km (100 km^2) squares, each divided into four 25-km^2 survey "blocks." Thus, the entire state was delineated into a total of 5,333 blocks. The operational definitions of possible breeding, probable breeding, and confirmed breeding are given, and there is a discussion of how the data were processed, including limitations and possible biases. The chapter concludes with 15 color maps that illustrate in great detail characteristics of the state, such as cities and major roads, river systems, and selected lakes (e.g., useful as landmarks); climate data such as precipitation and temperature; and habitat categories based on land use, forest types, and ecoregions. The latter is particularly useful for interpreting the distribution maps presented in the individual species accounts.

Chapter 2, by Kevin McGowan and Benjamin Zuckerberg, is a thorough comparison of the first and second surveys. Survey effort is quantified not only project wide, but also by region and by ecozone in relation to species richness. The heart of this chapter is the amount of change for each species, based on the number of blocks in which they were detected. This information is presented in two tables, the first arranged taxonomically for ease of finding a particular species, and the second in rank order of change. Additional tables are limited to those species in which the changes were statistically significant. An analysis of change with respect to breeding habitat revealed that grassland species by far had the greatest decline in distribution.

In Chapter 3, Gregory Endinger and Timothy Howard introduce the reader to the different habitats of the state, categorized by ecoregions, ecozones, bird conservation regions, and natural and cultural ecological communities. This chapter is followed by an examination of land-use changes, presented by Charles Smith and Peter Marks. Both chapters should be of interest to New York residents and nonresidents alike, and they help place the distribution changes into perspective. Chapter 5, by John Peterson, is a discussion of professional and amateur ornithology in New York and, in Chapter 6, Kenneth Rosenberg and Michael Burger identify conservation priorities regarding the state's breeding birds.

The main part of the book is the collection of species accounts, contributed by 41 authors. The text in each account consists of a brief introduction to the natural history of the species, its status from the first atlas, the changes that have occurred during the past 20 years, and conservation implications. There are two maps: one showing the 2000–2005 distribution, and the other the 20-year change. There also is a table that summarizes the number of blocks for which breeding was possible, probable, and confirmed in 1980–85 and 2000–05, and a graph that shows the USGS Breeding Bird Survey trend in New York from 1965 through 2005.

The layout is excellent. Each species account

covers two pages with the text and an attractive halftone portrait of the species on the left, and the maps, table, and graph on the right. Thus, the reader is presented each entire account without having to turn additional pages.

This book is a remarkable accomplishment. It belongs on the shelf of anyone interested in the changing distribution of birds in the northeastern United States. However, because the volume is so beautifully done, especially the 25 color paintings of New York habitats, it will be equally at home on the coffee table. Finally, at a time when college textbooks command over $100 for the paperback editions, the $59.95 list price for *The Second Atlas* represents a lot of value.—JOHN A. SMALLWOOD, Montclair State University, Montclair, NJ 07043, USA; e-mail: smallwoodj@montclair.edu

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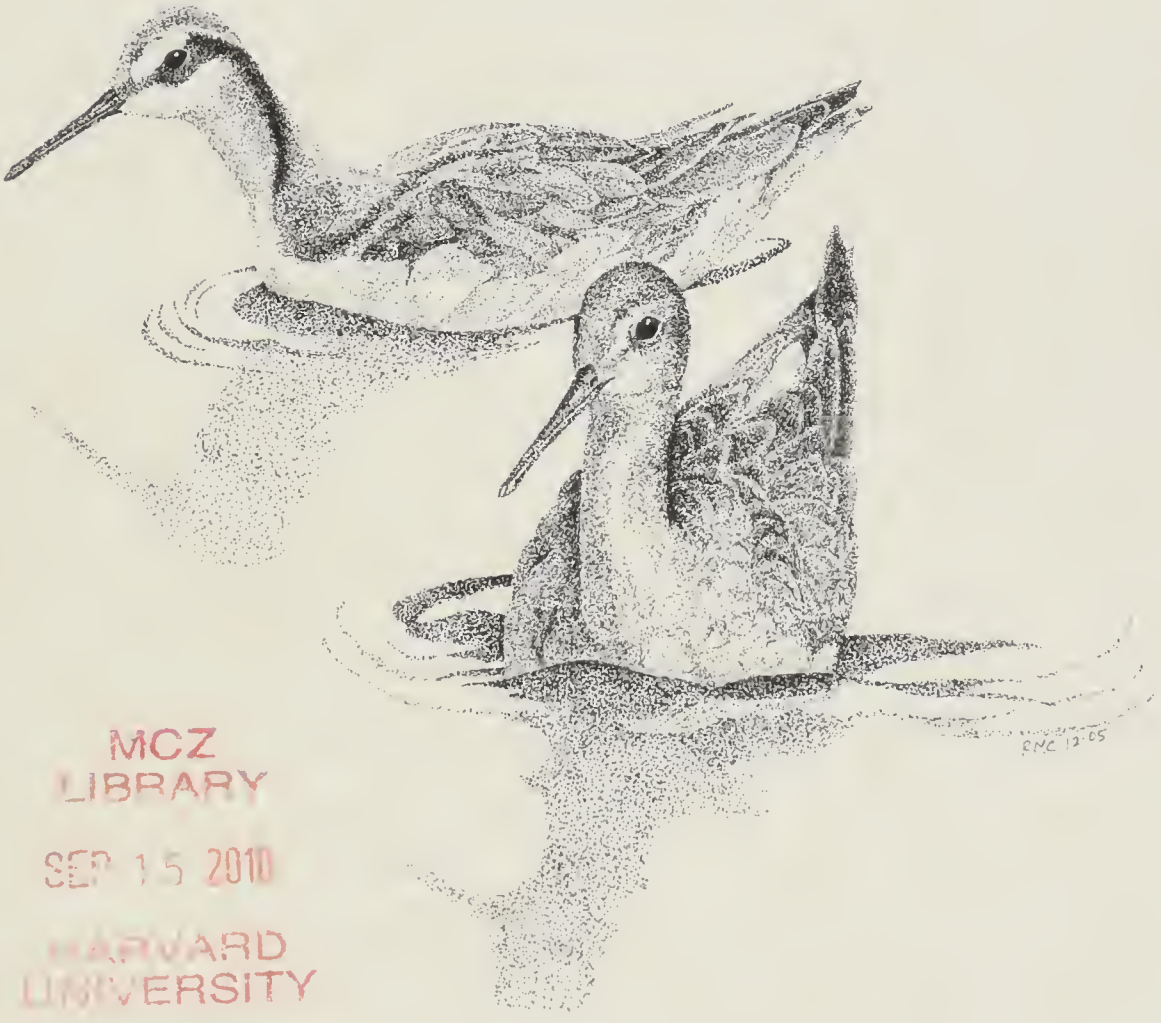

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COVER: Wilson's Phalaropes (*Phalaropus tricolor*). Illustration by Robin Corcoran.

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FRONTISPIECE. The Baywing (*Agelaioides badius*), an endemic species of southern South America, is the primary host of the most specialized of the parasitic cowbirds, the Screaming Cowbird (*Molothrus rufoaxillaris*). It is also a secondary host of the generalist Shiny Cowbird (*M. bonariensis*), which results in a rare, triangular host-parasite system. Photograph of an adult from the Province of Buenos Aires, Argentina by Alec Earnshaw.

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REPRODUCTIVE SUCCESS AND NESTLING GROWTH OF THE BAYWING PARASITIZED BY SCREAMING AND SHINY COWBIRDS

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ABSTRACT.—We studied the breeding biology of the Baywing (*Agelaioides badius*), a shared host of Screaming (*Molothrus rufoaxillaris*) and Shiny (*M. bonariensis*) cowbirds. We monitored 193 nests from December 2002 to March 2007 in the Province of Buenos Aires, Argentina. Baywings used a wide variety of nesting sites, mainly old nests of furnarids. Their breeding season lasted from late November to February and was closely matched by that of Screaming Cowbirds. The breeding season for Shiny Cowbirds started in late September but overlapped that of Baywings. Frequency and intensity of Screaming Cowbird parasitism were 93% and 5 eggs per parasitized nest, while for Shiny Cowbirds they were 16% and 1.4 eggs. Host clutch size was 4.0 ± 0.1 eggs and did not vary with time of breeding. Weight at hatching and age of maximum growth were similar for host and Screaming Cowbird nestlings. Shiny Cowbird nestlings had higher weight at hatching and lower age of maximum growth than the other two species. Screaming and Shiny cowbird nestlings had higher growth rates and asymptotic weights than host nestlings. Sex-specific growth curves of Screaming Cowbirds indicated males had higher growth rate and asymptotic weight than females. Only 19% of the nests produced fledglings. Host egg survival, hatching success, and nestling survival were 0.92, 0.88, and 0.94, respectively. Excluding nest failures, hosts fledged 0.78 chicks per egg laid. Baywings were smaller than Screaming and Shiny cowbirds, and experienced a high frequency and intensity of parasitism. However, the effect of parasitism on host hatching success and chick survival was low and comparable to that observed in larger hosts. *Received 1 September 2009. Accepted 8 March 2010.*

Obligate brood parasites lay their eggs in nests of individuals of other species (hosts), which provide all parental care for eggs and young. Brood parasitism in birds has evolved independently at least seven times, one of them in the genus *Molothrus*, within the New World icterine blackbirds (Lanyon 1992, Davies 2000, Sorenson and Payne 2002). This genus encompasses five parasitic species that show great variation in number of hosts they use (Ortega 1998). The basal species of the clade, the Screaming Cowbird (*M. rufoaxillaris*), is an extremely specialist parasite with only three known host species: Baywing (*Agelaioides badius*) (Hudson 1874, Friedmann 1929), Chopi Blackbird (*Gnorimopsar chopi*) (Sick 1985, Fraga 1996, Mahler et al. 2009), and the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) (Mermoz and Reboreda 1996, Mermoz and Fernández 2003). The Baywing is largely the primary host among these species with frequencies of parasitism often exceeding 80% of the

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nests (Mason 1980, Fraga 1998). In contrast, the Shiny Cowbird (*M. bonariensis*) is one of the most derived species (Lanyon 1992) and an extremely generalist parasite with more than 230 known hosts (Ortega 1998, Lowther and Post 1999). Shiny Cowbirds also parasitize Baywing nests but at a relatively low frequency (16–20% of the nests; Mason 1980, Fraga 1998). Screaming and Shiny cowbirds occasionally converge in Baywing nests resulting in an unusual three-sided host-parasite system (Fraga 1998).

There are several reports of Screaming and Shiny cowbird parasitism in nests of Baywings (Hudson 1874, Friedmann 1929, Mason 1980, Fraga 1998), but there are relatively few quantitative data on the breeding biology of this host and its interactions with both parasites. Previous studies indicate Baywings seldom build their nests, but exploit a wide variety of covered nesting sites, including old nests built by other species and holes in trees (Hoy and Ottow 1964, Fraga 1988). This nesting behavior has been proposed as an explanation for the late breeding of this species in Argentina (Friedmann 1929), where nesting attempts of Baywings typically occur from November to March (Fraga 1998). Baywings lay clutches of three to five eggs, but host eggs are often outnumbered by eggs of parasites (Hoy and Ottow 1964, Mason 1980, Fraga 1998, De Mársico and Reboreda 2008). The intensity of Screaming Cowbird parasitism in nests of Baywings is among the highest reported for a cowbird host (Mason 1986, Fraga 1998, Reboreda et al. 2003, Ellison et al. 2006, but see Kattan 1997, Trine 2000).

Multiple parasitism is likely to be costly for Baywings because Screaming and Shiny cowbirds often puncture host eggs during nest visits, which may reduce host clutch size even in unparasitized nests (Hoy and Ottow 1964, Fraga 1998, Massoni and Reboreda 2002, Astié and Reboreda 2006). Screaming and Shiny cowbirds, in addition, have a shorter incubation period than Baywings (Fraga 1998), which provides parasite nestlings a head start when parasitism is properly synchronized with host laying (Fraga 1998, Duré Ruiz et al. 2008, Fiorini et al. 2009). This increases the risk of host nestlings being outcompeted by larger cowbird nestlings (Payne and Payne 1998, Hoover 2003, Duré Ruiz et al. 2008).

Fraga (1986) estimated the effect of Screaming Cowbird parasitism on egg and nestling survival of Baywings. His estimates, however, may have overestimated the costs of parasitism because other sources of breeding failure such as nest predation were rare during his study (Fraga 1986). In addition, data of host and parasite nestling growth in Baywing nests are scarce. Fraga (1998) estimated growth parameters for Baywing and Screaming Cowbird nestlings, but his results did not account for non-independence among host nestlings from the same brood. Screaming and Shiny cowbirds also have a marked sexual size dimorphism (Mason 1987), but sex-specific growth curves of Screaming and Shiny cowbirds are lacking. Male and female parasite nestlings may have different growth patterns, and may differentially compete for food with host nestlings and experience different costs of competition (Weatherhead 1989, Tonra et al. 2008). Growth patterns of nestlings of both parasite species in Baywing nests have not been compared. Screaming and Shiny cowbird nestlings in nests of the Brown-and-yellow Marshbird, another shared host, did not differ in growth constant, asymptotic weight, and age of maximum growth (Mermoz and Fernández 2003); it remains unknown if the same is true for the primary host of the Screaming Cowbird.

Our objective was to use a large data set of 193 nests from five consecutive breeding seasons to examine: (1) quantitative data on several aspects of the nesting biology of the Baywing, (2) baseline estimates of host reproductive success and nest productivity, and (3) novel data on nestling growth in Baywing nests, providing the first report of sex-specific growth curves of Screaming and Shiny cowbirds.

METHODS

Study Area.—Our study was conducted from December 2002 to March 2007 at the private reserve El Destino near Magdalena (35° 08′ S, 57° 23′ W) in Buenos Aires Province, Argentina. The study site is a flat area of 320 ha within the Biosphere Reserve Parque Costero del Sur (MAB-UNESCO). Vegetation comprises woodland patches dominated by *Celtis tala* and *Scutia buxifolia* surrounded by grasslands and marshes (Cagnoni et al. 1996). Baywings are year-round residents in this area.

Potential nesting sites for Baywings within our study area included old nests of other species and cavities in trees. We placed 50 wood nest boxes between 2002 and 2003 to facilitate data collection. Boxes were 30 × 20 × 16 cm (height, width,

and depth), and had a 58-mm diameter circular entrance hole and a removable roof to allow nest inspection. All boxes were attached to trees at the edge or in the interior of woodland patches at heights of 1.8–2.5 m. Nest boxes were separated by at least 50 m. Previous observations indicated that Baywings did not use empty boxes, and we partially filled them with artificial nests of wood sticks and plant fibers. One hundred additional nest boxes, similar yet smaller than those for Baywings (25 × 17 × 13 cm in height, width, and depth, entrance hole = 45 mm), were placed in the area (also attached to trees at a height of 1.2–1.8 m) starting in 2003 and were also available to Baywings. Most of these boxes had inactive House Wren (*Troglodytes aedon*) nests by the time Baywings started breeding. All nest boxes were cleaned prior to the beginning of each breeding season, and the large ones were re-filled with new artificial nests.

Data Collection.—We looked for Baywing nests throughout each breeding season (mid Nov–late Feb). Most nests were found along edges of woodland patches or in isolated trees at heights of 1.3–10 m. We limited our study to those nests at heights < 5 m, which could be inspected using a portable ladder. Nest boxes were checked twice each week to detect any new nesting attempt. We recorded whether each nest was in a natural site or a nest box. We classified natural sites by identity of the nest builder when it was known, or the nest architecture.

Active nests (i.e., nests with a defending pair of Baywings) were checked every 1–3 days until they fledged chicks or failed. We assigned each nest an initiation date, corresponding to laying of the first Baywing egg. This date was ascertained directly when the nest was found before or during host laying, or indirectly through backdating from hatching dates (considering an incubation period of 13 days since the laying of the penultimate egg; Fraga 1998), when the nest was found during incubation. We examined the nest contents during each visit taking all eggs and nestlings from the nest. Individual eggs were assigned to the host or each parasite species on the basis of background color, spotting pattern, and shape (Friedmann 1929; Fraga 1983, 1986). Maximum width and length of host and parasite eggs were measured to the nearest 0.1 mm using a vernier caliper. Hatchlings of each species were identified using skin and bill coloration as diagnostic cues (Friedmann 1929; Fraga 1979, 1986). We assigned the laying date of Screaming and Shiny cowbird eggs either directly or through backdating from hatching dates (incubation period: 12 days for both species; Fraga 1998) whenever possible. We assumed that laying in half of the cases occurred the same day the egg was found, and in the other half the eggs were laid the previous day when nests were inspected every other day and the parasite egg appeared between two successive visits. All eggs and nestlings were marked with waterproof ink for identification. Nestlings were weighed daily or every other day to the nearest 0.1 or 0.5 g using Pesola spring scales of 10- and 60-g capacity, respectively. We visited nests at approximately the same hour of the day whenever possible to record weights at regular daily intervals. All nestlings were banded at 10–11 days of age with a unique combination of color leg bands and a numbered aluminum band.

We took a small amount (15–30 µL) of blood from a subsample of parasite nestlings at 8 to 11 days of age through brachial vein puncture with a 31G needle. Blood was collected with an 80 µL heparinized capillary tube, immediately mixed with 0.5 mL of lysis buffer (100mM Tris pH 8, 10 mM NaCl, 100mM EDTA, 2% SDS) and stored at room temperature until analysis. Individuals were identified as male or female genetically following Ellegren (1996). DNA was extracted from blood samples using a standard salting-out protocol (Miller et al. 1988) and diagnostic sex-linked alleles were amplified using the P8/P2 primer set (Griffiths et al. 1998). Amplifications were performed in 10 µL reaction volumes using 50–100 ng of DNA template, 0.5 µM forward and reverse primers, 0.25 µM dNTPs, 2.5 mM $MgCl_2$, and 0.25 u Taq-Polymerase. Annealing temperatures were set at 50° C and repeated for 30 cycles. PCR products were separated in 3% agarose gels stained with ethidium bromide. The presence of one band indicated males (ZZ), whereas two bands indicated females (ZW).

We stopped visiting nests once nestlings were banded and blood-sampled to avoid inducing premature fledging. However, we continued observing the nest daily or every other day from a distance of 5–10 m to identify the date of fledging. Host and parasite fledglings typically remain in the natal territory for at least 3 weeks (Fraga 1991), and we could confidently identify whether young fledged successfully or not.

We artificially parasitized 56 Baywing nests with fresh Shiny Cowbird eggs (n = 51) or newly

hatched nestlings ($n = 5$) obtained from parasitized Chalk-browed Mockingbird (*Mimus saturninus*) and House Wren nests. Shiny Cowbird eggs laid in Chalk-browed Mockingbird and House Wren nests did not differ in width from those in Baywing nests (ANOVA: $F_{2,98} = 2.3$, $P = 0.10$; D. T. Tuero, unpubl. data). However, eggs from Chalk-browed Mockingbird nests were longer (ANOVA: $F_{2,98} = 8.7$, $P < 0.001$) and had greater volume (ANOVA: $F_{2,98} = 5.8$, $P < 0.004$) than those in nests of the other two host species (Tukey *post-hoc* test: $P < 0.05$; D. T. Tuero, unpubl. data). Artificially parasitized nests were checked as described above, and data on eggs and nestlings were collected in the same way as in naturally parasitized nests.

Data Analysis.—Frequency of parasitism was calculated as number of nests with parasite eggs or chicks over total number of nests found and intensity of parasitism as number of parasitic eggs per parasitized nest. Overall intensity of parasitism was estimated using a subset of nests found before or during host laying to avoid underestimating the number of cowbird eggs that were laid asynchronously and later removed from the nest cup by Baywings (Hoy and Ottow 1964, Fraga 1998, De Mársico and Reboreda 2008). We compared the intensity of parasitism among years for each cowbird species using the Kruskal-Wallis test. Data from 2002 were excluded for the analysis corresponding to Shiny Cowbirds because only one of the parasitized nests was found early in the nesting cycle. We used the Kolmogorov-Smirnov test for two independent samples (Siegel and Castellan 1989) to compare the frequency distribution of Baywing nesting attempts and frequency of parasitic events of Screaming Cowbirds during the breeding season (divided into weekly intervals). We estimated the extent of overlap between the breeding seasons of Baywings and Shiny Cowbirds using laying dates of parasite eggs in nests of Baywings ($n = 23$) and of two primary hosts in the study area, Chalk-browed Mockingbird ($n = 335$ eggs) and House Wrens ($n = 176$ eggs). Data on laying dates for these species were collected during 2003, 2006, and 2007 (V. D. Fiorini and D. T. Tuero, unpubl. data).

We estimated clutch size of Baywings using a subsample of 32 nests found before laying, visited daily during laying, and which survived at least until laying ended. We used these criteria to avoid missing egg losses because hosts often remove punctured eggs (Massoni and Reboreda 2002, Astié and Reboreda 2006). We estimated total clutch size from nests parasitized after the host began to lay that survived until hatching. We used two estimates: initial clutch size, defined as the number of host and parasite eggs that remained in the nest by the end of host laying, and final clutch size, defined as the number of host and parasite eggs by the end of incubation. Host incubation period was estimated as the number of days elapsed since laying of the last host egg until hatching of the last host chick (Nice 1954). The incubation period of Screaming and Shiny cowbird eggs was estimated as the number of days elapsed since the start of incubation until the day of hatching of the parasite chick (Briskie and Sealy 1990). We calculated the number of parasite chicks at hatching from nests that were parasitized during host laying that survived until the nestling stage.

We calculated egg volume (cm^3) for host, and Screaming and Shiny cowbirds as $0.515\ l\ w^2$, where l and w are egg length and width (in cm); 0.515 is a species specific constant (Nolan and Thompson 1978). Measures of Baywing eggs were averaged over host clutch for statistical analyses. The sample of Shiny Cowbird eggs included those in Baywing nests ($n = 11$) as well as those in nests of Chalk-browed Mockingbird ($n = 61$) and House Wrens ($n = 29$) from the same study area (D. T. Tuero, unpubl. data).

Growth curves were built using data from nestlings that survived at least 10 days and were weighed daily or every other day. Nestlings that were depredated or died in the nest were excluded from the analyses. We used non-linear regressions to adjust daily weights of each nestling following the logistic function for weight: $W = A/(1 + \exp(-K*(T - T_0)))$, where A is the asymptotic weight, K is the growth constant and T_0 is the age of maximum growth (Ricklefs 1967). Regressions used a non-linear model and least-squares estimation minimized with the Quasi-Newton option in SYSTAT 9.0 (SPSS, Chicago, IL, USA). Parameter estimates and weight at hatching were obtained for each individual nestling from the adjusted curves. Maximum growth rate (g_{max}) was calculated using the expression: $g_{max} = K * A/4$ (Richner 1991). Host nestlings from the same brood were not independent, and growth parameter estimates of individual nestlings from the same nest were averaged to generate a growth curve for each brood. We used data from 69

Baywing nestlings in 25 nests (5 broods with 1, 4 with 2, 9 with 3, 6 with 4, and 1 with 5 nestlings) to build growth curves. Five broods were unparasitized, 12 were parasitized by Screaming Cowbirds only (9 with 1, and 3 with 2 parasitic chicks), three were parasitized by Shiny Cowbirds only (each with a single parasitic chick), and five had one chick of each parasite species. Mean (± SE) brood size was 4.0 ± 0.3 chicks per brood, including host and parasite chicks. We obtained growth data for 18 Screaming Cowbird nestlings from 13 broods (10 with 1, 3 with 2, and 1 with 5 Screaming Cowbird chicks). These broods had, on average, 2.9 ± 0.4 host chicks (range = 0–4), and three also had one Shiny Cowbird chick. Mean brood size was 4.7 ± 0.4 chicks per brood (range = 1–8). Data from Screaming Cowbird chicks from the same brood were averaged. We also obtained growth data for 10 Shiny Cowbird nestlings from 10 different broods. These broods had, on average, 3.4 ± 0.7 host chicks (range = 2–5), and four were also parasitized by Screaming Cowbirds (3 with 1, and 1 with 2 Screaming Cowbird chicks). Mean brood size was 4.9 ± 0.3 (range = 3–6). We ascertained the gender of 10 Screaming (6 females and 4 males) and seven Shiny (5 females and 2 males) cowbird nestlings. We used this subsample to obtain sex-specific growth parameters of each parasite species, but comparisons of growth parameters among Baywing, and Screaming and Shiny cowbird nestlings used the full data set.

The date of fledging was established directly in a few cases where we observed the fledglings leaving the nest. Chicks in most nests fledged between two successive visits, and we assumed that in half of the cases they did it the same day we observed them out of the nest, and in the other half, that they fledged 1 day earlier.

We estimated nest survival as the proportion of nests that produced at least one host or parasite fledgling. Host and parasite reproductive success was estimated using three parameters: (1) egg survival, calculated as the proportion of host or parasite eggs that survived until the end of incubation in nests that survived until the nestling stage; (2) hatching success, calculated as the proportion of host or parasite eggs that hatched from those that survived; and (3) chick survival, calculated as the proportion of host or parasite chicks that fledged from those that hatched in nests that survived the entire nesting cycle. Survival of parasite eggs was estimated from nests found before or during host laying that survived until hatching. We considered as parasitized those clutches that received cowbird eggs during laying or incubation to analyze the effect of parasitism on egg survival and hatching success. We considered as parasitized those nests with parasite chicks to analyze the effect of parasitism on nestling survival. Counts included parasitic eggs or chicks artificially placed in Baywing nests. Overall host productivity in successful nests was estimated as the number of host chicks fledged divided by host clutch size. Productivity of Screaming and Shiny cowbirds was estimated as the number of parasite chicks fledged divided by the total number of parasite eggs laid in nests that were found before or during host laying and survived until fledging, including those that were laid before the beginning of host laying. Only naturally parasitized nests were considered to estimate productivity.

Statistical tests followed GenStat Discovery Edition 3 (GenStat 2007) and results are presented as $\bar{x} \pm$ SE. All tests are two tailed and significance was accepted at $P < 0.05$.

RESULTS

Nest Site Use.—We found 193 Baywing nests. Eighty-nine (46%) were in old, closed nests made of sticks built by species of the Furnariidae (e.g., *Anumbius annumbi*, *Phacellodomus* spp., *Synallaxis* spp.), 40 (21%) in large nest boxes, 16 (8%) in old Rufous Hornero (*Furnarius rufus*) nests, 16 (8%) in old Great Kiskadee (*Pitangus sulphuratus*) nests, 14 (7%) in cavities in trees, 10 (5%) in small nest boxes previously used by House Wrens, five (3%) were open cup-nests built by Baywings, and three (2%) were in unusual nesting sites (an old Chalk-browed Mockingbird nest, a broken tree branch, and an old nest of the paper wasp [*Polybia scutellaris*]). There were no differences among years in frequency of nests found in natural or artificial nesting sites ($\chi^2_4 = 6.6$, $P = 0.16$).

Considering nests with known clutch initiation date ($n = 116$), the median date of clutch initiation differed among nest types, indicating that use of nest sites varied during the breeding season (Kruskal-Wallis test: $H_5 = 13.9$, $P = 0.017$, $n = 12$ Great Kiskadee nests, 27 nest boxes, 9 natural cavities, 53 old furnarid nests made of sticks, 7 Rufous Hornero nests, and 8 nests of other types). *Post-hoc* comparisons indicated that old Great Kiskadee nests were

TABLE 1. Clutch and brood composition at Baywing nests in the Reserve El Destino (2002–2006). Bw = unparasitized nests, Bw + Sc = nests parasitized by Screaming Cowbirds only, Bw + Sh = nests parasitized by Shiny Cowbirds only, and Bw + Sc + Sh = nests parasitized by both species. Only naturally parasitized nests with known clutch size were considered for egg and chick counts. Values represent number of eggs or nestlings of each species as $\bar{x} \pm$ SE and the corresponding sample sizes (number of nests).

	Bw	Bw + Sc	Bw + Sh	Bw + Sc + Sh
Eggs laid				
Bw	4.1 ± 0.3 (12)	3.7 ± 0.1 (142)	0 (1)	3.8 ± 0.2 (21)
Sc		4.9 ± 0.3 (142)		4.6 ± 0.5 (21)
Sh			1.0 (1)	1.2 ± 0.1 (21)
Eggs incubated				
Bw	4.6 ± 0.2 (7)	3.5 ± 0.1 (80)		3.6 ± 0.3 (11)
Sc		2.4 ± 0.2 (49)		1.8 ± 0.4 (21)
Sh				0.6 ± 0.2 (21)
Young at hatch				
Bw	4.4 ± 0.2 (5)	3.2 ± 0.2 (49)		2.8 ± 0.5 (6)
Sc		1.0 ± 0.1 (49)		1.0 ± 0.4 (6)
Sh				0.7 ± 0.3 (6)
Young fledged				
Bw	4.7 ± 0.3 (3)	2.9 ± 0.2 (28)		2.7 ± 0.9 (3)
Sc		1.2 ± 0.2 (28)		0.3 ± 0.3 (3)
Sh				0.3 ± 0.3 (3)

occupied significantly later than small nest boxes ($P < 0.05$). Baywings used non-active nests in most cases, but in two cases we observed usurpation of active nests (1 nest of Firewood-gatherer [*Anumbius anumbi*] and 1 nest box occupied by House Wrens). Only five nests in our sample were built by Baywings; all were open cup nests with a lax structure of grasses and a 'roof' provided by surrounding foliage.

Nest reuse occurred both within and among breeding seasons. We observed nest reuse in 51/51 cases within breeding seasons when the nest failed due to clutch ejection by hosts in response to multiple parasitism, but we only observed nest reuse in 1/46 cases when the nest failed due to predation. We observed nest reuse in 11 cases among breeding seasons (nest sites that were used in 2 or more consecutive breeding seasons), although we could not establish if the same breeding pair was involved. Reuse occurred in five of these cases in nests that had been successful in the previous breeding season whereas in the others, the nest failed in the previous breeding season.

Incidence of Cowbird Parasitism.—Ninety-four percent of the nests (181/193) were parasitized, 155 by Screaming Cowbirds only, one by Shiny Cowbirds only, and 25 by Screaming and Shiny cowbirds. Frequency of parasitism did not differ among years (Screaming Cowbird: $\chi^2_4 = 0.38$, $P = 0.98$; Shiny Cowbird: $\chi^2_4 = 7.19$, $P = 0.13$). There were no differences in frequency of parasitism combining data from all years between natural nests ($n = 153$) and nest boxes ($n = 40$) for Screaming ($\chi^2_1 = 1.44$, $P = 0.76$) and Shiny ($\chi^2_1 = 0.52$, $P = 0.47$) cowbirds.

Average intensity of parasitism was 5.0 ± 0.3 eggs for Screaming Cowbirds ($n = 140$ nests) and 1.4 ± 0.1 eggs for Shiny Cowbirds ($n = 19$ nests; Table 1). We did not detect differences among years in intensity of parasitism by Screaming (Kruskal-Wallis test: $H_4 = 5.9$, $P = 0.21$) or Shiny (Kruskal-Wallis test: $H_4 = 3.3$, $P = 0.34$) cowbirds; the later result should be interpreted cautiously given the small sample size. Pooling data from all years indicated the intensity of Screaming Cowbird parasitism did not differ between natural nests ($n = 98$) and nest boxes ($n = 42$; Mann-Whitney U-test: $Z = -0.31$, $P = 0.76$). Similarly, the intensity of Shiny Cowbird parasitism did not differ between natural nests ($n = 11$) and nest boxes ($n = 8$; Mann-Whitney U-test: $Z = -0.61$, $P = 0.54$).

Screaming Cowbirds parasitized Baywing nests either before, during, and after host laying. On average, a parasitized nest received 1.3 ± 0.3

Screaming Cowbird eggs before host laying, 1.2 ± 0.2 during host laying, 1.1 ± 0.2 eggs during the incubation stage, and 0.4 ± 0.1 eggs after nestlings had hatched (n = 39 parasitized nests found before or during host laying that survived until the nestling stage). Eggs laid before host laying were removed from the nest by Baywings before they started to lay. Eggs laid after the host began laying were accepted and incubated, but only those laid during host laying typically hatched. Shiny Cowbirds also parasitized Baywing nests either before or during host laying. Nests received, on average, 0.8 ± 0.6 and 0.5 ± 0.6 Shiny Cowbird eggs before and during host laying, respectively (n = 18 parasitized nests).

Breeding Seasons.—The earliest and latest clutch initiation dates for Baywings were 27 November and 7 February, respectively. The first Screaming Cowbird parasitism was recorded on 26 November (in a nest at pre-laying stage) and the latest on 11 February (Fig. 1). The frequency of Screaming Cowbird parasitism matched the frequency distribution of Baywing nesting attempts in all breeding seasons (Kolmogorov-Smirnov test: $P > 0.10$ for all comparisons; Fig. 2).

The earliest Shiny Cowbird parasitism event was recorded on 29 September in a Chalk-browed Mockingbird nest and the latest, on 23 January in a Baywing nest. Even though Shiny Cowbirds started laying earlier than Baywings, they overlapped considerably in breeding seasons (Fig. 3). Shiny Cowbird parasitism mostly (44%) occurred in December and January. Nearly 90% of all Baywing clutches were initiated during the same interval. Only 10% of Baywing nesting attempts began too late to be parasitized by Shiny Cowbirds.

Clutch Size, Incubation, and Nestling Periods.—Baywings laid, on average, 4.0 ± 0.1 eggs per nest (range = 2–5, mode = 4, n = 32 nests), and host clutch size did not vary with clutch initiation date (Spearman rank correlation: r = 0.22, Z = 1.23, P = 0.23, n = 32 nests). Initial clutch size in nests parasitized solely by Screaming Cowbirds was 5.3 ± 0.2 eggs, and final clutch size was 6.4 ± 0.2 eggs (n = 49 nests). Only two nests naturally parasitized by Shiny Cowbirds survived until hatching, and they were also parasitized by Screaming Cowbirds. Initial clutch size in these nests was 7.0 ± 1.0 eggs, and final clutch size was 8.0 ± 1.0 eggs (Table 1).

Host incubation period was 13.0 ± 0.1 days with a range of 12–14 days and a mode of 13 (n = 42 clutches). Screaming and Shiny cowbirds had an incubation period of 12.0 ± 0.1 days (range = 11–13 days, n = 40 and 14 eggs of Screaming and Shiny cowbirds, respectively). Average number of Baywing chicks at hatching was 3.2 ± 0.1 (range = 0–5, n = 60). Nests parasitized by Screaming Cowbirds only, had 1.3 ± 0.2 parasite chicks at hatching (n = 37). Nests naturally parasitized by Shiny Cowbirds (n = 2) had one Shiny Cowbird and one Screaming Cowbird chick each. Combining host and parasitic chicks, Baywings reared, on average, 4.2 ± 0.2 chicks per nest (range = 1–8, n = 60 nests; Table 1). The mean nestling period was 14 days (range = 12–16; n = 20 nests).

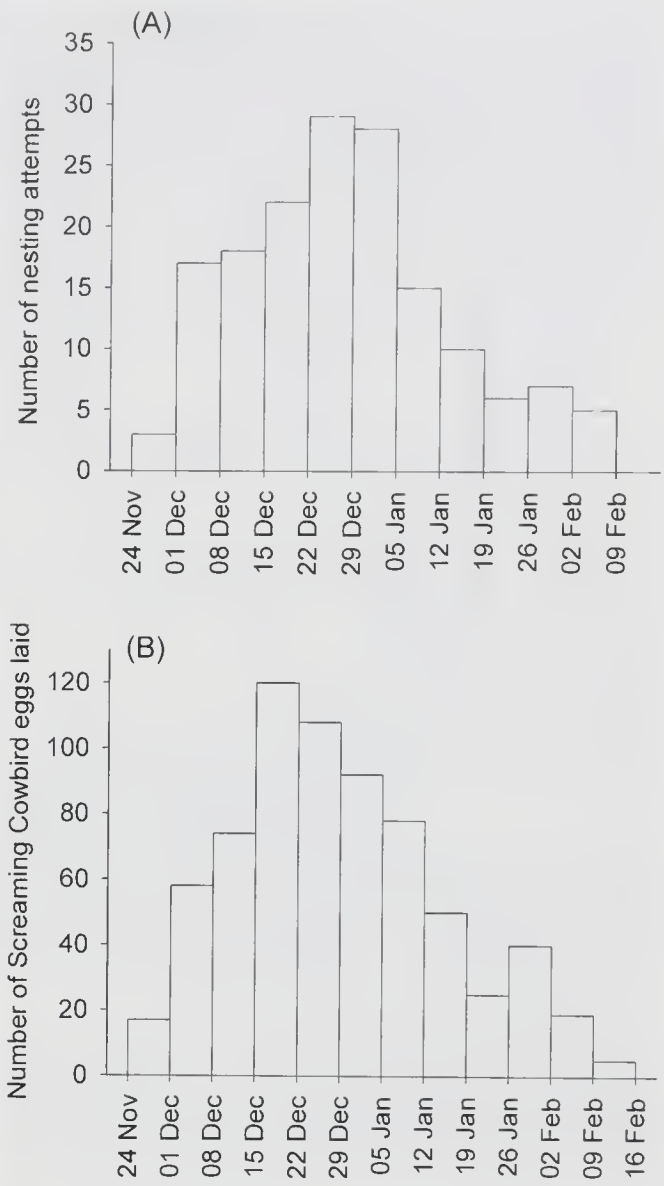

FIG. 1. Breeding season of (A) Baywings and (B) Screaming Cowbirds in Reserve El Destino between 2002 and 2006. Bars represent the number of nesting attempts initiated (n = 160) or the total number of Screaming Cowbird eggs laid (n = 686) during the breeding season divided into weekly intervals.

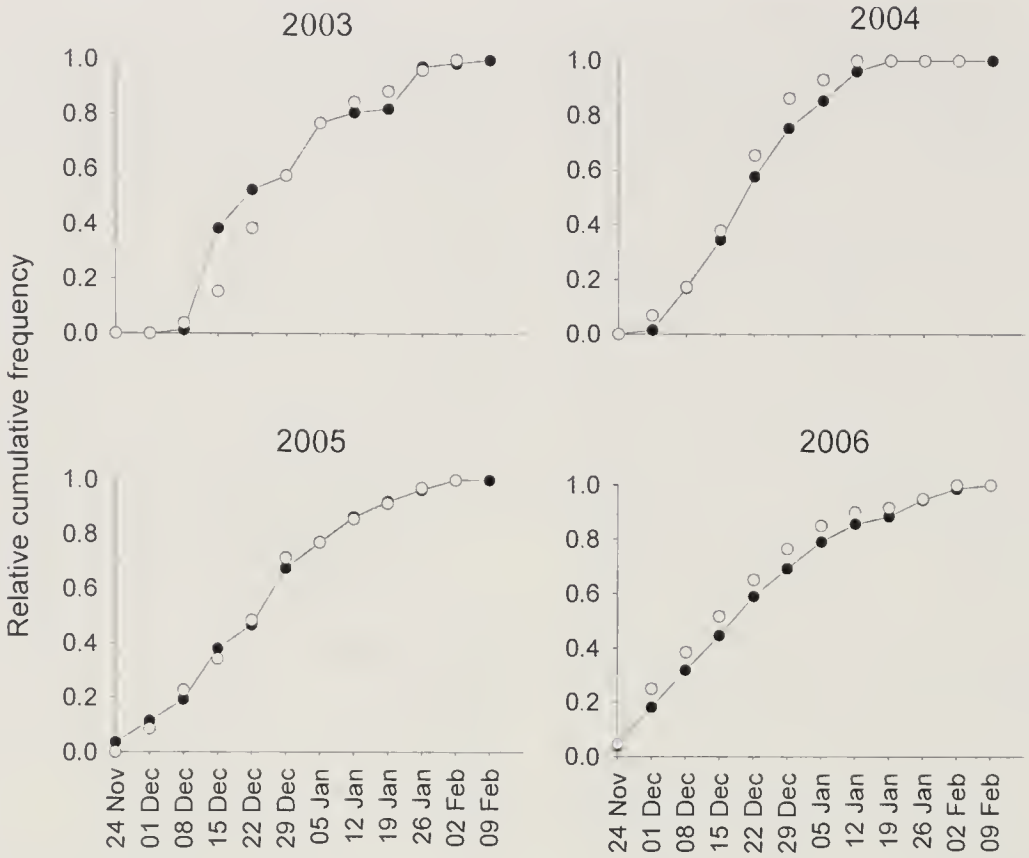

FIG. 2. Baywing and Screaming Cowbird breeding seasons. Curves represent the cumulative relative frequency of Baywing nesting attempts (white) and parasite eggs laid (black) along the breeding season. Sample sizes are: 2003 = 26 nests and 78 eggs, 2004 = 29 nests and 130 eggs, 2005 = 35 nests and 139 eggs, and 2006 = 60 nests and 312 eggs. Year 2002 was excluded due to small sample sizes.

Egg Size and Nestling Growth.—Egg size and volume differed between host and parasites (Table 2). Shiny Cowbird eggs were wider than those of Baywings and Screaming Cowbirds (ANOVA: $F_{2,552} = 76.8$, $P < 0.001$) and had greater volume (ANOVA: $F_{2,552} = 52.2$, $P < 0.001$; Tukey *post-hoc* test: $P < 0.05$). Egg length did not differ among species (ANOVA: $F_{2,552} =$

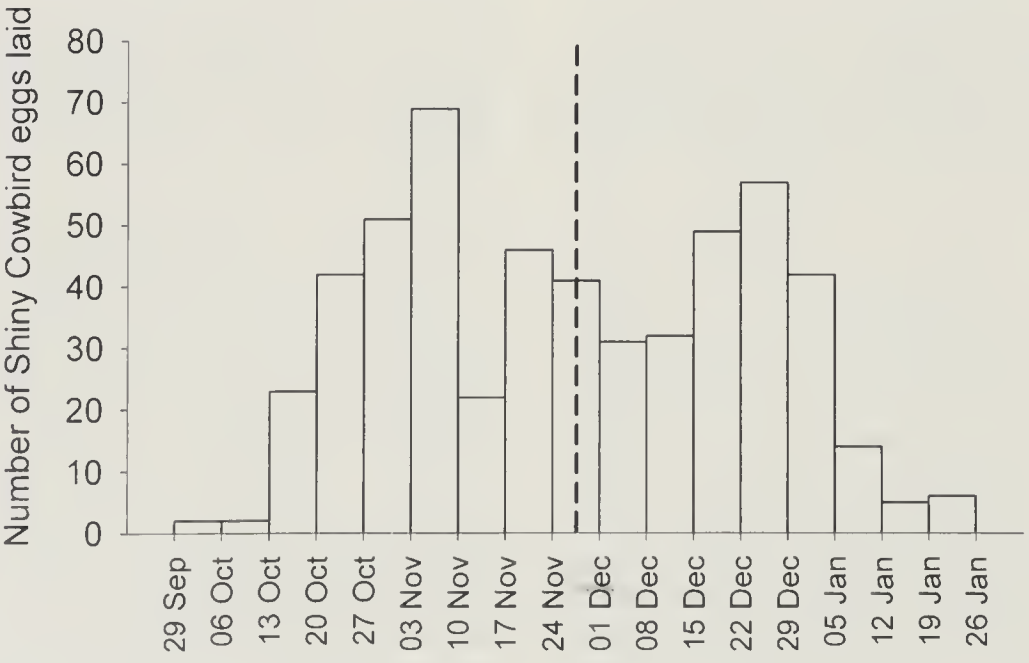

FIG. 3. Seasonal distribution of Shiny Cowbird parasitism in Reserve El Destino during the 2002–2006 breeding seasons. Bars represent the number of parasite eggs laid within each weekly interval in nests of Baywings, Chalk-browed Mockingbirds, and House Wrens ($n = 534$). The dashed line indicates clutch initiation date of the earliest Baywing nesting attempt during this study (27 Nov).

TABLE 2. Length, width, and volume ($\bar{x} \pm$ SE) of Baywing, and Screaming and Shiny cowbird eggs. Values corresponding to host eggs represent average egg size and volume of all eggs in 98 clutches. Some Baywing (Bw) nests in our sample were artificially parasitized with Shiny Cowbird eggs collected from Chalk-browed Mockingbird (CbM) and House Wren (HW) nests, and we present data on size and volume of Shiny Cowbird eggs in the three host species. Data from Chalk-browed Mockingbird and House Wren nests were provided by V. D. Fiorini and D. T. Tuero (unpubl. data).

Species	Host	*n*	Length (cm)	Width (cm)	Volume (cm^3)
Baywing		346	2.36 ± 0.01	1.78 ± 0.00	3.87 ± 0.02
Screaming Cowbird	Bw	357	2.37 ± 0.01	1.79 ± 0.00	3.94 ± 0.02
Shiny Cowbird	Bw	11	2.30 ± 0.03	1.86 ± 0.00	4.11 ± 0.16
	CbM	61	2.43 ± 0.02	1.89 ± 0.01	4.49 ± 0.05
	HW	29	2.34 ± 0.00	1.86 ± 0.00	4.20 ± 0.10

1.6, $P = 0.20$). Differences in egg volume were not attributable to larger Shiny Cowbird eggs coming from Chalk-browed Mockingbird nests because the results did not change when these eggs were removed from the data set (ANOVA: $F_{2,491} = 8.9$, $P < 0.001$).

We found differences in growth parameters between host and parasite chicks, as well as between Screaming and Shiny cowbird chicks (Table 3, Fig. 4). Overall, both Screaming and Shiny cowbirds had higher growth constant (ANOVA: $F_{2,45} = 6.5$, $P = 0.003$), maximum instantaneous growth rate (ANOVA: $F_{2,45} = 45.8$, $P < 0.001$), and asymptotic weight ($F_{2,45} = 37.3$, $P < 0.001$) than Baywing nestlings (Tukey *post-hoc* test, $P < 0.05$). Shiny Cowbirds had a higher weight at hatching (ANOVA: $F_{2,45} = 6.7$, $P = 0.003$) and lower age of maximum growth ($F_{2,45} = 8.8$, $P < 0.001$; Tukey *post-hoc* test, $P < 0.001$) than both Screaming Cowbird and host nestlings.

Sex-specific growth curves for Screaming and Shiny cowbirds varied (Table 3, Fig. 4). Male Screaming Cowbird nestlings ($n = 4$) did not differ from females ($n = 6$) in weight at hatching (*t*-test: $t = -1.15$, df = 8, $P = 0.28$), growth constant (*t*-test: $t = -0.09$, df = 8, $P = 0.93$), and age of maximum growth (*t*-test: $t = -0.46$, df = 8, $P = 0.66$; Table 3). However, male nestlings had a higher maximum instantaneous growth rate (*t*-test: $t = -3.84$, df = 8, $P = 0.005$) and reached a higher asymptotic weight than females (*t*-test: $t = -5.53$, df = 8, $P < 0.001$; Table 3). Sample sizes for Shiny Cowbirds were too low for statistical analyses, but growth curves suggest that differences in males and females similar to those of Screaming Cowbirds might occur in this species (Table 3, Fig. 4).

Baywing Reproductive Success.—Only 35 (19%) of all nests fledged chicks and all but one produced host fledglings. The exception was a parasitized nest where all host eggs failed to hatch and only two Screaming Cowbird chicks fledged. The number of Baywing chicks fledged per nest was 3.0 ± 0.2 ($n = 34$ nests, range = 1–5). Overall, host productivity in nests that survived the entire nesting cycle was 0.78 fledglings per egg laid ($n = 25$ nests with known clutch size). Losses were mostly due to egg punctures by Screaming and Shiny cowbirds and hatching failures. On average, survival of host eggs was 0.92 ($n = 54$ nests). Egg survival was higher in

TABLE 3. Growth parameters ($\bar{x} \pm$ SE) of Baywing, and Screaming and Shiny cowbird nestlings obtained from adjusted growth curves. Data for host nestlings were averaged over each brood. Data for parasite nestlings were based on individual nestlings of each gender. Sample sizes = 69 Baywings in 25 broods, 6 female and 4 male Screaming Cowbirds, and 5 female and 2 male Shiny Cowbirds.

Parameter	Baywing	Screaming		Shiny	
		Male	Female	Male	Female
Hatch weight, g	3.6 ± 0.1	3.8 ± 0.4	3.3 ± 0.2	4.9 ± 0.3	4.4 ± 0.2
Growth constant/day	0.47 ± 0.01	0.50 ± 0.02	0.49 ± 0.02	0.51 ± 0.03	0.51 ± 0.03
Maximum growth rate, g/day	4.25 ± 0.07	6.37 ± 0.14	5.23 ± 0.22	6.10 ± 0.14	5.31 ± 0.32
Age of maximum growth, days	5.8 ± 0.1	6.2 ± 0.2	6.0 ± 0.2	5.3 ± 0.2	5.2 ± 0.1
Asymptotic weight, g	36.7 ± 0.4	51.6 ± 1.9	42.5 ± 0.6	48.3 ± 1.8	41.4 ± 1.0

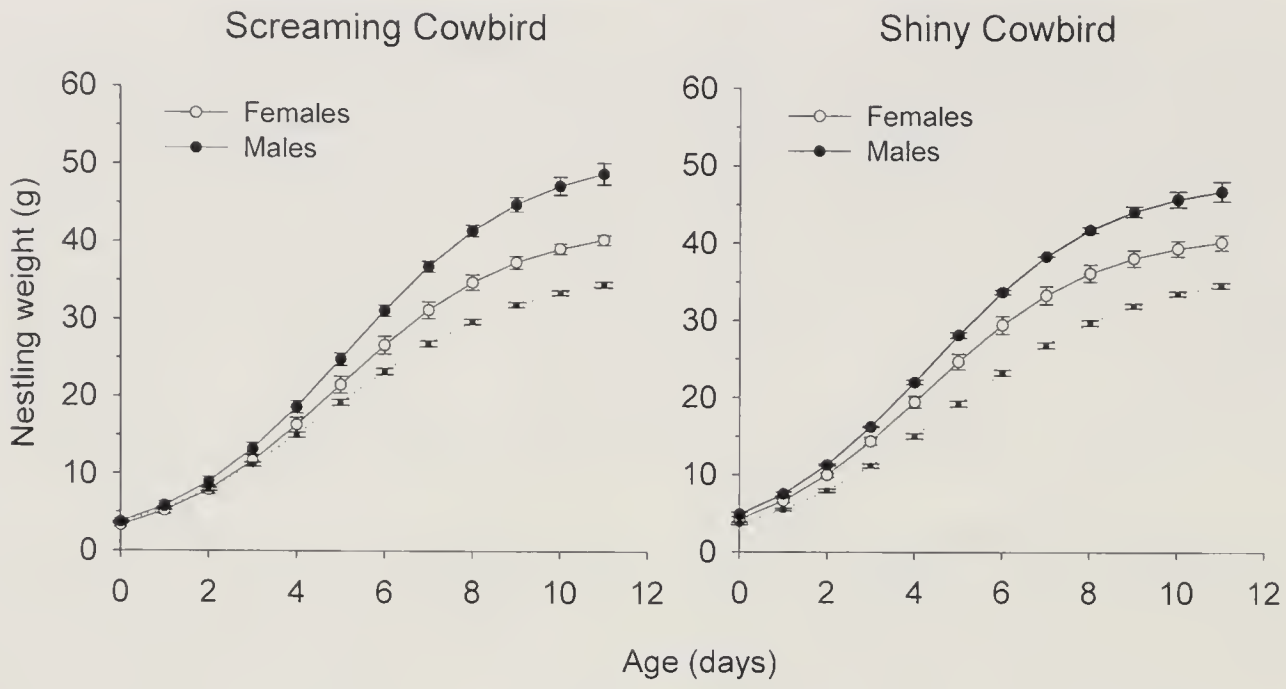

FIG. 4. Growth curves of Screaming and Shiny cowbird nestlings reared by Baywings. Points correspond to daily weights ($\bar{x} \pm$ SE) as a function of age for male (black circles) and female (white circles) nestlings of each species, estimated from the corresponding adjusted logistic functions. The dotted line in each graph represents the growth curve of the host with adjusted daily weights ($\bar{x} \pm$ SE) averaged across all host nestlings within the same brood (n = 25 broods with 1–5 host nestlings) Sample sizes were four and six female Screaming Cowbirds, and two and five female Shiny Cowbirds, respectively.

nests that were not parasitized during the egg stage than in parasitized nests (Mann-Whitney U-test: $Z = -2.03$, $P = 0.042$, $n = 10$ unparasitized and 44 parasitized nests). On average, hatching success was 0.88 ($n = 54$ nests). Hatching success did not differ between parasitized and unparasitized nests (Mann-Whitney U-test: $Z = 0.00$, $P > 0.99$). There were no statistical differences in survival of Baywing chicks between parasitized ($n = 20$) and unparasitized nests ($n = 8$; Mann-Whitney U-test: $Z = -1.52$, $P = 0.13$). Nestling survival was, on average, 0.94 ($n = 28$ nests). Brood reduction occurred in six parasitized nests where one ($n = 5$) or two ($n = 1$) host nestlings died due to starvation or nest crowding.

Screaming Cowbird Reproductive Success.—About 89% (615/694) of the Screaming Cowbird eggs in Baywing nests failed as a result of nest predation or desertion ($n = 146$ naturally parasitized nests found before or during host laying). Survival of Screaming Cowbird eggs in nests that survived until hatching was 0.93 ($n = 48$ nests). Hatching success was 0.62 ($n = 47$ nests), and hatching failures were mostly due to parasitic females laying eggs too late for successful incubation. Hatching success of Screaming Cowbird eggs laid during host laying was 0.92 ($n = 40$ nests). Overall nestling survival was 0.77 ($n = 20$ nests). Mortality of parasitic chicks occurred at six nests as a result of late hatching ($n = 4$ nests) and partial nest predation ($n = 2$ nests). Screaming Cowbird productivity was 0.14 fledglings per egg laid ($n = 20$ nests).

Shiny Cowbird Reproductive Success.—Nearly 91% of Shiny Cowbird eggs naturally laid (30/33, $n = 26$ nests) and 82% of those artificially placed in Baywing nests (40/49, $n = 49$ nests) failed due to nest predation or desertion. Combining natural and artificial parasitism, Shiny Cowbird egg survival was 0.95 ($n = 19$ nests) and hatching success was 0.94 ($n = 18$ nests). Nestling survival was 0.91 ($n = 11$ nests) and only one Shiny Cowbird chick died, presumably due to partial nest predation. Sample size was too small to estimate productivity. Only one of three Shiny Cowbird eggs naturally laid produced a fledgling ($n = 3$ nests). The others were laid before host laying and therefore rejected by hosts.

DISCUSSION

Nest Site Use.—Baywings used a wide variety of nesting sites, but the more commonly used were old, closed nests built by several furnarid species. This observation contrasts with a previous study in a nearby area, which reported that

nest boxes and secondary cavities were preferred nesting sites (Fraga 1988, 1998). These differences, however, could be explained by local variation in abundance of suitable nesting sites at the time Baywings start to breed (Hoy and Ottow 1964). Some authors have observed Baywings fighting with owners to occupy their nests (Friedmann 1929, Jaramillo and Burke 1999), but we seldom observed nest piracy, suggesting that nesting sites were not limiting during our study (see also Hoy and Ottow 1964, Fraga 1988). It is not clear why in most cases Baywings use old nests of other species instead of building their own nests, but it is possible this behavior allows breeding pairs to save time and energy (Hauber 2002, Wiebe et al. 2007). Additionally, closed nests might offer better protection against predators than open cup nests (Martin and Li 1992, Auer et al. 2007).

Breeding Seasons.—Our results indicate the breeding season of Baywings typically starts in early December and may extend to early March, considering nestling and postfledgling stages of late nesting attempts. Fraga (1998), in the Province of Buenos Aires, observed laying as early as October, but we did not observe any sign of nesting activity before late November. The breeding season of Screaming Cowbirds overlapped extensively that of Baywings. However, female Screaming Cowbirds started parasitism in advance of host laying indicating that nest building and defense activities by the host may stimulate laying behavior of the parasite. It is also possible the parasite's breeding season began earlier if Screaming Cowbirds in our study area also parasitize Brown-and-yellow Marshbirds, which breed from October to December (Mermoz and Reboreda 1996, Mermoz and Fernández 2003). Shiny Cowbirds began to breed much earlier in our study area than Baywings, parasitizing other hosts such as Chalk-browed Mockingbirds and House Wrens starting in late September (Fiorini and Reboreda 2006, Tuero et al. 2007).

Friedmann (1929) suggested differences in time of breeding would be the cause of the low frequency of Shiny Cowbird parasitism in nests of Baywings. However, our data indicate only 10% of the nesting attempts of Baywings began after the Shiny Cowbird breeding season ended. Breeding seasons of Baywings and Shiny Cowbirds overlapped more extensively than previously estimated (90 vs. 65–80%; Fraga 1998), and female Shiny Cowbirds would have broad opportunities for parasitizing this host. An alternative explanation for the low frequency of Shiny Cowbird parasitism of this host is that the parasite would have low reproductive success with Baywings (Fraga 1998), but this hypothesis remains untested.

Incidence of Cowbird Parasitism.—Nearly all Baywing nests were parasitized by Screaming Cowbirds, and regularly more than once (Hoy and Ottow 1964, Mason 1980, Fraga 1998). These high levels of parasitism did not seem to be an artifact of nest boxes (Kattan 1997), as the frequency and intensity of parasitism by Screaming and Shiny cowbirds did not differ between nest boxes and natural sites. Our results did not appear to be influenced by the shortage of host nests in a particular year, as frequency and intensity of parasitism were consistent among consecutive breeding seasons. Females of other brood parasites parasitize nests within nearly exclusive breeding areas, which may allow them to reduce the costs associated with intraspecific competition (Langmore et al. 2007). Several observational and genetic studies indicate that cowbirds, however, lack territorial behavior (Kattan 1997, Hahn et al. 1999, Mermoz and Reboreda 1999, McLaren et al. 2003, Strausberger and Ashley 2005, Ellison et al. 2006). Thus, multiple parasitism can arise as a consequence of a limitation of suitable nests, high fecundity rates of female cowbirds, or high population density of the parasite relative to the number of host breeding pairs (Martínez et al. 1998, Strausberger 1998, McLaren et al. 2003, Ellison et al. 2006). Multiple parasitism by Screaming Cowbirds, which are constrained to locate and parasitize near a single host species, could also be the result of different females parasitizing the same nest and individual females parasitizing a nest more than once as a result of low nest availability.

Baywing Reproductive Success.—Cowbird parasitism reduces host fitness in several ways (Massoni and Reboreda 1998, Lorenzana and Sealy 1999, Zanette et al. 2005, Astié and Reboreda 2006). We found parasitized nests lost more host eggs than unparasitized nests, but hatching success and nestling survival did not differ between parasitized and unparasitized nests. Our results indicate survival of Baywing eggs and nestlings was higher than in previous reports (Fraga 1986, 1998), possibly because, during our study, most host egg and nestlings were lost due to nest desertion and predation rather than to egg punctures or competition with parasite nestlings.

We rarely observed brood reduction in parasitized nests and nestling mortality due to parasitic mites, as reported previously (Fraga 1986). Regular cleaning of nest boxes may have contributed to decrease the incidence of ectoparasite infestations in our study population. However, given that most nests occurred in natural sites, we have confidence that box cleaning had little influence on our estimates of nestling survival. Costs of parasitism for Baywings are similar to those observed in other host species of the Shiny Cowbird that are larger than the parasite (Mermoz and Reboreda 2003, Astié and Reboreda 2006). Productivity is often lowered in hosts larger than the parasite by puncture or removal of host eggs by female cowbirds rather than by nestling mortality, as host young are seldom outcompeted by parasitic nestlings (Eckerle and Breitwisch 1997, Lichtenstein 1998, Lorenzana and Sealy 1999, Astié and Reboreda 2006), unless a marked hatching asynchrony exists (Soler et al. 1996, Duré Ruiz et al. 2008). Baywings are smaller than Screaming and Shiny cowbirds; thus, it is expected that host nestlings compete strongly for food with the parasite young. However, Baywings are cooperative breeders (Fraga 1991) and it is possible that helpers at the nest contribute to ameliorate the costs of parasitism by increasing nest provisioning rates (Fraga 1991).

Nestling Growth.—We did not find differences in growth patterns between Screaming and Shiny cowbird nestlings in nests of Baywings. Overall, Screaming and Shiny cowbird nestlings did not differ in asymptotic weight, growth constant, and maximum instantaneous growth rate. This is consistent with similar comparisons between parasite nestlings of both species reared in Brown-and-yellow Marshbird nests (Mermoz and Fernández 2003). However, parasite nestlings differed in weight at hatching and age of maximum growth, which could be the result of differences in egg size between both species (Nolan and Thompson 1978). A higher weight at hatching combined with a shorter incubation period could provide Shiny Cowbird nestlings a head start to overcome competition, which can be particularly important in nests of host species larger than the parasite (Astié and Reboreda 2006, Fiorini et al. 2009). However, evidence for a positive effect of egg size on nestling performance is equivocal (e.g., Schifferli 1973, Magrath 1992, Reed et al. 1999).

Screaming Cowbird eggs and hatchlings were similar in mass to those of Baywings, although parasitic juveniles and adults are quite larger than the host (Mason 1987, Fraga 1998). Females in other parasite species have evolved eggs similar in size to those of the host, presumably in response to host discrimination against larger or smaller eggs (Mason and Rothstein 1986, Marchetti 2000). No experiments have been conducted on Baywings to test whether they are able to discriminate eggs by size. However, that they readily accepted larger Shiny Cowbird eggs artificially placed in their nests (this study) suggests Baywings do not discriminate foreign eggs on the basis of size. Screaming Cowbird eggs in Baywing nests usually have low chances of success as a consequence of poor synchronization of parasitism and high nest failure rates (Hoy and Ottow 1964, Fraga 1998, De Mársico and Reboreda 2008). Thus, a selective pressure may exist on female Screaming Cowbirds to increase the total number of eggs laid at the expense of laying smaller eggs (Fontaine and Martin 2006, Martin et al. 2006).

Screaming Cowbird nestlings were sexually dimorphic in size and presented sex-specific growth curves. Males grew faster and were larger than females over the entire nestling period, consistent with a recent study of Brown-headed Cowbirds (*Molothrus ater*) (Tonra et al. 2008, but see Weatherhead 1989). Our sample sizes were too small to compare growth parameters between male and female Shiny Cowbirds, but our data indicate that sex-specific growth patterns similar to that observed in Screaming Cowbirds may occur in this species. The occurrence of sex-specific growth curves among parasitic cowbirds implies that gender should be considered when analyzing the costs of competition and factors affecting nestling growth in host and parasite species.

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BOBOLINK EGG MASS VARIABILITY AND NESTLING GROWTH PATTERNS

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ABSTRACT.—The Bobolink (*Dolichonyx oryzivorus*) is an obligate grassland species that is declining throughout its range in North America. There are few data available on Bobolink eggs and nestlings; this information is necessary for conservation planning efforts. Egg mass was recorded for 175 eggs from 37 nests in Québec and eastern Ontario in 2006–2007. Hatching asynchrony was evident with high between-clutch variation in egg mass. Egg mass did not differ with clutch size. Nest initiation date was positively correlated with smallest egg size and negatively correlated with within-clutch egg mass deviation. Nestling wing length, tarsus length, and mass were measured for 166 nestlings ranging from 2 to 10 days of age. Bobolink nestlings fledged below adult size and mass, achieving 87.7 ± 2.3%, 67.6 ± 1.5%, and 55.1 ± 0.4% of breeding adult tarsus length, mass, and wing length (± SE), respectively. *Received 13 December 2008. Accepted 4 February 2010.*

The Bobolink (*Dolichonyx oryzivorus*) is an obligate grassland species that has recently received attention concerning population declines, mainly due to habitat loss and agricultural intensification (Bollinger et al. 1990, Herkert 1997). Studies have examined aspects of breeding ecology (e.g., Bollinger and Gavin 1992, Winter et al. 2004), but little information is available on eggs and nestlings, including linear nestling measurements. In addition, reported values are based on small sample sizes (e.g., mean egg mass, $n = 5$; Martin and Gavin 1995).

Nestling growth rates and patterns in passerines are useful measures to examine the influence of environmental, parental, and social parameters to which the nestlings are subject. Knowledge of a time-frame of critical growth for body components may provide insight into vulnerable periods during the nesting cycle. Nestling growth may be affected by pre-hatching (e.g., egg mass and incubation) and post-hatching factors. Egg mass variability may result from physiological differences among females or environmental variables such as geographic location, weather, and food availability (Christians 2002). As first hypothesized by Lack (1967), a trade-off exists between clutch size and egg size; females have a limited amount of energy for egg production that must be shared between the number of eggs and size of the eggs. In addition, some species exhibit seasonal change in egg size (Magrath 1992) or seasonal effects of within-clutch egg size variability (Takagi 2003).

Nestling growth patterns may be described using several different parameters: (1) growth rate, (2) percent of adult weight attained by dependent young in the nest, and (3) shape of the growth curve (Ricklefs 1968a). Standard growth rate curves show mass increasing throughout the nestling period and reaching near-adult weights at fledging. There are two alternate curves where (a) nestlings attain a peak mass above adult weight and decrease to adult weight just before or after fledging, and (b) growth levels remain below adult values at fledging (Ricklefs 1968a). Growth rates may vary between individual broods of the same species, but growth patterns are species-specific (Ricklefs 1968a). For example, nestlings that fledge above adult weight are primarily oceanic species and aerial insectivores with long nestling periods, and are independent feeders post-fledging (Ricklefs 1968b). Conversely, ground-feeding species fledge below adult weight and rely on well-developed legs for escaping predators (Ricklefs 1968b).

The goal of our study was to identify patterns and variability of egg mass and nestling growth in a population of Bobolinks by comparing: (1) egg mass within- and between clutches; (2) the relationship between (a) clutch size and egg mass and (b) nest initiation date and egg mass; (3) nestling growth between years of study, study sites and between broods; and (4) Bobolink nestling growth patterns by percentage of adult size and mass attained at fledging.

METHODS

Study Area.—This study was conducted in 2006–2007 at three sites in southwestern Québec

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and eastern Ontario with established Bobolink populations. The sites consisted of a private hay farm near Hemmingford, Québec (45° 05′ N, 73° 36′ W), an agricultural park (Bois-de-la-Roche) in Senneville, Québec (45° 26′ N, 73° 56′ W), and a wildlife conservation area (Atocas Bay) in Lefaivre, Ontario (45° 36′ N, 74° 51′ W). All sites consisted of multiple hayfields dominated by timothy (*Phleum pratense*) and smooth brome (*Bromus ramosus* ssp. *racemosus*) at Hemmingford, and a broader mixture of forbs and grasses at Atocas and Bois-de-la-Roche.

Measurements.—We measured and numbered eggs on day of discovery or as they were laid, and weighed them to the nearest 0.1 g with a portable electronic balance. We took nestling measurements twice during consecutive visits 3–4 days apart between 0700 and 1500 hrs EST. We marked individual nestlings on the initial visit by coloring their toenails using non-toxic permanent markers. Nestlings were separately classified by age during each visit, as asynchronous hatching resulted in different ages of nestlings within the same nest. Nestling age was classified using a combination of external physical traits: amount of down, feather tracts, feather eruption from sheaths, and opening of eyes. Photos were taken at each visit and compared to known-age nestlings to confirm classification. We measured length of the unflattened wing (wing length) to the nearest 0.5 mm using a ruler with a wing stop, and tarsometatarsus (tarsus) length to the nearest 0.1 mm with dial calipers. We weighed nestlings to the nearest 0.1 g. The same person performed all measurements to reduce observer bias. We banded nestlings at ≥ 7 days of age using aluminum bands. We monitored all nests until completion, and nests that fledged at least one young were recorded as successful.

Statistical Analysis.—We checked egg and nestling data for normality using Shapiro-Wilks' test (Zar 1999). All measurements were normally distributed, allowing use of untransformed data in subsequent analyses. We compared egg mass between years using Student's *t*-test and between sites using one-way ANOVA (Zar 1999). We examined the variance of egg mass between and within clutches using one-way ANOVA. We examined if mean egg mass per clutch varied with changes in nest initiation date using linear regression. We also examined the variance of mean egg mass with clutch size using one-way ANOVA. We examined the effect of initiation date on mass of the smallest egg in each clutch using linear regression. We used the standard deviation of mean egg mass per clutch as a measure of within-clutch egg mass variation. We regressed standard deviations with Julian initiation date to examine if within-clutch variation changed with initiation date of the nest.

We measured a subset (n = 102) of nestlings twice over the span of 10 days, obtaining a mixed longitudinal sample of nestling growth (Ricklefs 1983). We measured the remaining nestlings once (n = 64). We calculated mean age measurements for nestling wing length, tarsus length, and mass from 2 to 10 days of age, and examined variance across all ages using ANOVA. We used nested ANOVA in which year of study, study site, and brood were nested within nestling age. Missing values for day 8 at Bois-de-la-Roche, and day 10 for both Bois-de-la-Roche and Atocas were replaced with mean values for those dates. We calculated the percent of adult size and mass that was reached each day of nestling growth. Individual nestling measurements were divided by adult measurements, giving a percentage of adult growth. These were averaged to acquire mean (± SE) percentage of adult growth for nestlings of 2–10 days of age.

Male and female Bobolinks are dimorphic, but cannot be assigned to gender without genetic testing as nestlings. Thus, we averaged the reported adult male and female measurements from the breeding season to use as general adult measurements (Martin and Gavin 1995). We reported all mean values ± SE and used SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and JMP 8.0.1 (SAS Institute Inc., Cary, NC, USA) for all analyses.

RESULTS

Hatching Phenology and Egg Measurements.—Three of 25 nests for which nestling measurements were obtained hatched synchronously (12%); 20 nests had one marginal nestling (80%), and two nests had two marginal nestlings (8%). Nestlings in three of four re-nests were each 1 day apart in age.

Measurements were taken for 175 eggs from 37 nests. Sixteen of the 53 nests monitored were excluded from egg calculations as they were found either during the nestling stage or depredated prior to measurements being taken. Mean egg mass over both years and all sites (n = 175) was 2.69 ± 0.05 g (1.6–3.5 g). We found no

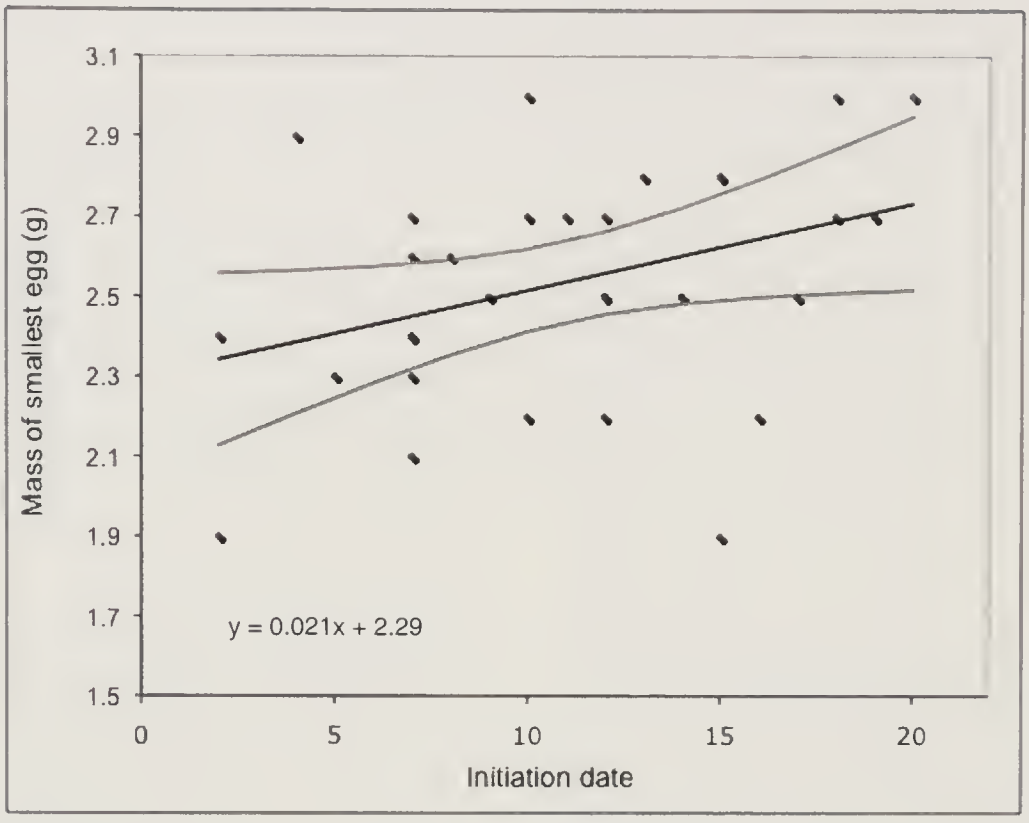

FIG. 1. Linear regression with 95% CI of smallest egg mass in Bobolink clutch compared to initiation date at Atocas Bay, Ontario, Bois-de-la-Roche, Québec, and Hemmingford, Québec during 2006 and 2007.

differences between Bobolink egg mass between years of study ($T_{175} = -1.87$, $P = 0.062$) and among study sites ($F_{175} = 1.45$, $P = 0.24$).

We found a between-clutch effect of egg mass across Bobolink females ($F_{37} = 13.089$, $P < 0.001$). The model sum of squares accounted for between-clutch variation only (12.773) and the total sum of squares accounted for both between- and within-clutch variation (16.824). Thus, between-clutch variation accounted for 75.9% of the total variation.

We found no differences in egg mass between clutch sizes ($F_{37} = 0.830$, $P = 0.487$) and mean egg mass was not related with initiation date ($r^2 = 0.088$; $F_{37} = 1.89$, $P = 0.10$). Egg mass of the smallest egg in the clutch increased with initiation date ($r^2 = 0.13$; $F_{37} = 4.390$, $P = 0.045$, $\beta = 0.021 \pm 0.01$ SE; Fig. 1). Within-clutch egg mass variation was not related to clutch size ($F_{37} = 0.246$, $P = 0.863$), but decreased with greater date of nest initiation ($r^2 = 0.277$; $F_{37} = 11.500$, $P = 0.002$; Fig. 2).

Nestling Measurements and Growth.—We report mean ± SE nestling measurements for nestlings at ages 2–10 days (Table 1). Bobolink nestlings had ~ 5–10% larger tarsi in 2007 than in 2006 ($F_{268} = 8.871$, $P < 0.001$) and ~ 10–15% more mass in 2007 than in 2006 ($F_{268} = 3.620$, $P < 0.001$). Wing length did not differ between years ($F_{268} = 1.382$, $P = 0.204$). Year of study had an impact on two of the three variables tested; we tested among study sites within each year to prevent possible year effects. None of the variables for 2006 differed among study sites: nestling wing length ($F_{268} = 1.221$, $P = 0.279$), tarsus length ($F_{268} = 0.518$, $P = 0.898$), and mass ($F_{268} = 0.530$, $P = 0.890$). However, all variables differed among sites in 2007: nestling wing length ($F_{268} = 1.859$, $P = 0.033$), tarsus length ($F_{268} = 1.838$ $P = 0.036$), and mass ($F_{268} = 2.330$, $P = 0.005$). Among site-differences were most evident between younger nestlings with Atocas > Bois-de-la-Roche > Hemmingford nestlings; there were no differences among sites at nestling age 8–10 days. All variables in all years differed between individual broods.

Nestling growth as a percentage of adult size and mass increased predictably across nestling age (Fig. 3). Nestlings for all variables were below adult size or mass at day 10, just prior to or at fledging. Nestling measurements as percentage of adult ± SE at day 10 were: wing length = 55.1 ± 0.4%, tarsus length = 87.7 ± 2.3%, and mass = 67.6 ± 1.5%.

DISCUSSION

Asynchronous Hatching.—Hatching asynchrony was prevalent in the Bobolink population we studied. Most nests (80%) had a single late-

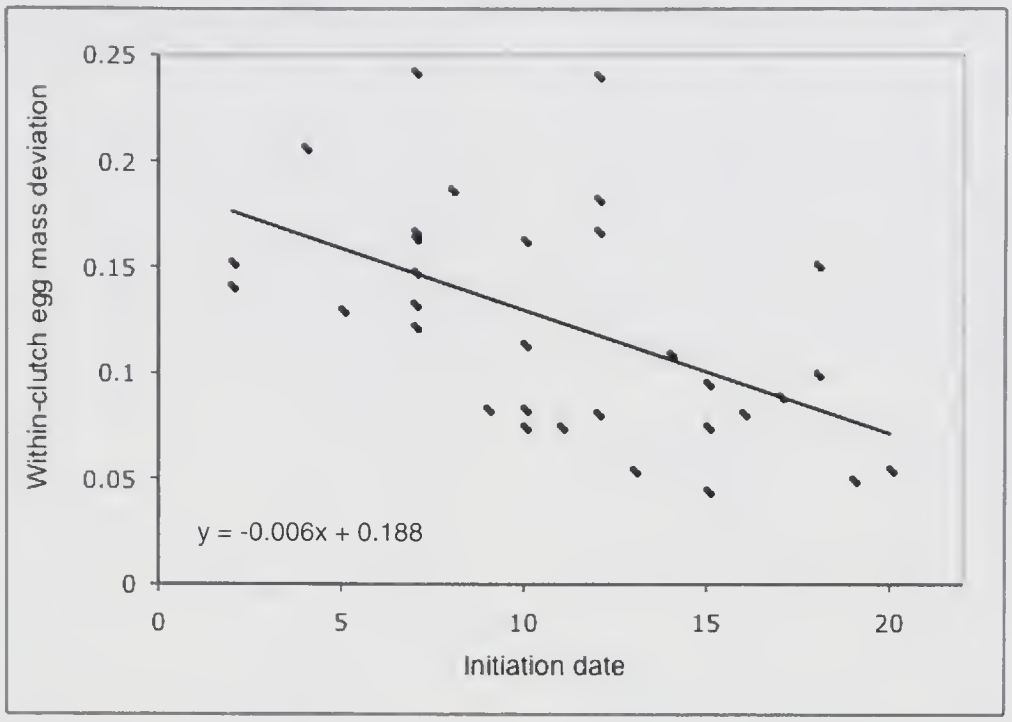

FIG. 2. Linear regression showing within-clutch deviation of Bobolink egg mass compared to initiation date at Atocas Bay, Ontario, Bois-de-la-Roche, Québec, and Hemmingford, Québec during 2006 and 2007.

hatched nestling, resulting from incubation beginning with the penultimate egg, as previously described for Bobolinks (Martin 1974). Few nests had two late-hatched nestlings (8%), far fewer than in the closely related Red-winged Blackbird (*Agelaius phoeniceus*) where 8.1% of nests hatched synchronously, 41.9% had one late-hatched nestling, and 43.3% had two late-hatched nestlings (Forbes and Glassey 2000). Three of four re-nests in our study had nestlings staggered in age, a result of incubation beginning with the first egg laid. This, paired with smaller clutch size, suggests females shorten the re-nesting cycle as Bobolinks rarely re-nest (Martin and Gavin 1995).

Egg Mass Variation Within- and Between Clutches.—Between-clutch variation of egg mass far exceeded within-clutch variation. This pattern is common for most bird species with an average of 70% of variation in egg size due to variation between- rather than from within-clutches (Christians 2002). Egg size appears to reflect differences among individual females, and often increases with age and experience (Christians 2002). Overall, consistency of egg and clutch size is a consequence of selective pressures and energy expenditure limitations (Lack 1947).

Egg Mass Variation with Clutch Size and Nest Initiation Date.—Our data did not support Lack's (1967) trade-off hypothesis that greater energy

TABLE 1. Mean (± SE) wing, tarsus, and mass measurements for Bobolink nestlings (n = 268) at Atocas Bay, Ontario, Bois-de-la-Roche, Québec, and Hemmingford, Québec during 2006 and 2007.

Nestling age (days)	n	Wing length (cm)	Tarsus length (cm)	Mass (g)
2	6	1.02 ± 0.03	0.95 ± 0.03	6.5 ± 0.6
3	24	1.28 ± 0.04	1.08 ± 0.04	7.4 ± 0.3
4	47	1.78 ± 0.04	1.31 ± 0.04	10.0 ± 0.3
5	39	2.38 ± 0.05	1.67 ± 0.04	14.2 ± 0.3
6	39	3.00 ± 0.05	1.86 ± 0.05	16.4 ± 0.3
7	33	3.34 ± 0.08	2.07 ± 0.09	17.3 ± 0.8
8	46	4.22 ± 0.06	2.22 ± 0.03	19.9 ± 0.9
9	27	4.72 ± 0.04	2.33 ± 0.04	21.5 ± 0.4
10	7	5.10 ± 0.04	2.25 ± 0.06	21.6 ± 0.5

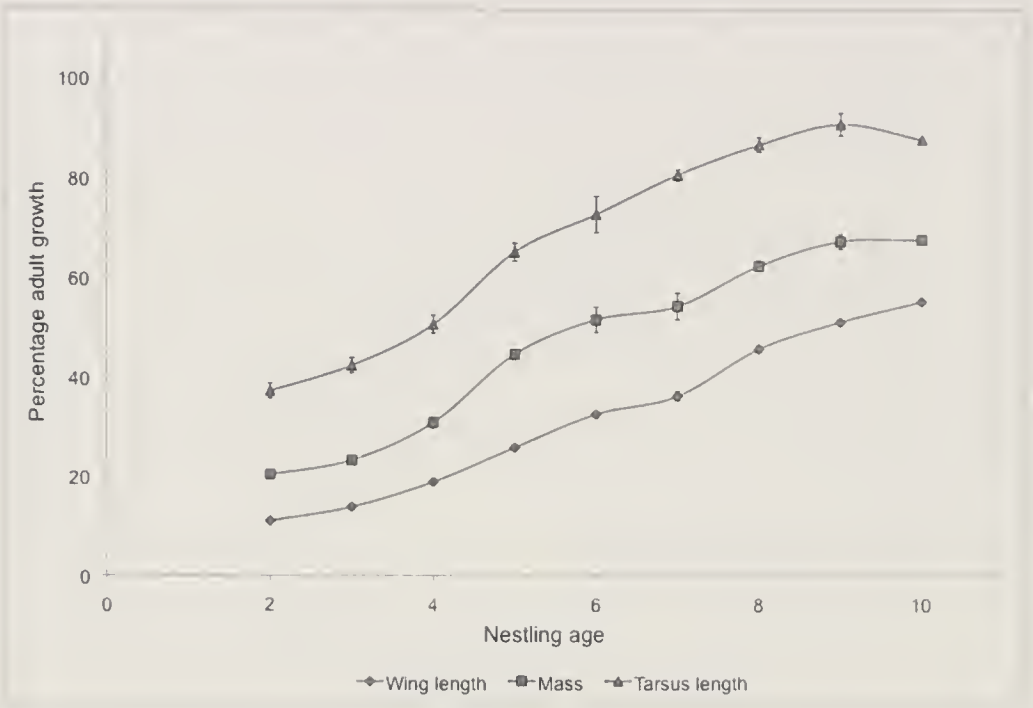

FIG. 3. Nestling growth represented as a percent of breeding adult Bobolink measurements ± SE for wing length, tarsus length, and mass for Bobolink nestlings pooled for sites and years.

expenditure during laying results in larger clutches of smaller eggs. This hypothesis has been empirically supported in several studies (Blackburn 1991, Olsen et al. 1994), but others have failed to find a negative relationship between clutch size and egg size (Rohwer and Eisenhauer 1989). The opposite has been demonstrated to be true, in some cases, where smaller clutches contain smaller eggs (Galbraith 1988).

Female Bobolinks appear to have laid larger eggs more consistently as the nesting season progressed, as nest initiation date was positively correlated with egg mass of the smallest egg and negatively correlated with within-clutch variation. In temperate regions, such as eastern Canada, ambient temperature increases throughout the breeding season resulting in decreased daily energy expenditure for homeotherms and increased food availability for insectivores (Avery and Krebs 1984, Reeva et al. 2000). In turn, this relaxes energy expenditure constraints related to egg-laying activities and may result in larger eggs later in the season. Mean egg mass of Common Blackbirds (*Turdus merula*) was correlated with air temperature during the period when the species was undergoing rapid follicular growth (Magrath 1992), and Great Tits (*Parus major*) roosting in heated nest boxes laid larger eggs than those in cooled nest boxes (Nager and Zandt 1994).

Few studies have investigated within-clutch seasonal variation of egg size. Takagi (2003) in northern Japan during a study of Bull-headed Shrikes (*Lanius bucephalus*) found a seasonal increase in intra-clutch variation of egg volume due to a seasonal size decline in the smallest egg within the clutch. The inverse was true in the Bobolinks we studied; within-clutch variation decreased as the mass of the smallest egg increased over the season. Bobolinks in our study area began laying from mid- to late May. It is often cool and rainy during this period resulting in high energetic costs for laying females, leading to smaller smallest eggs and higher within-clutch variation earlier in the breeding season. Common Swifts (*Apus apus*) similarly lay lighter eggs during unfavorable weather (O'Conner 1979).

Nestling Growth.—Bobolink young at fledging were well below adult size and mass. Thus, the Bobolink growth curve is a variant of the 'standard' growth curve in which growth levels off below adult weight (Ricklefs 1968a). Bobolink young are often described as poor flyers for several days post-fledging (Martin and Gavin 1995), a result of leaving the nest prior to full feather emergence. Eastern Meadowlarks (*Sturnella magna*) (Lanyon 1995) and Savannah Sparrows (*Passerculus sandwichensis*) (Wheelwright and Rising 2008) are also ground-nesting grassland birds that fledge at below adult mass. This may be adaptive for ground-nesting birds, whose young are especially vulnerable to predators and disturbance. Nestlings of species with

well-protected nests generally remain in nests longer than young in exposed nests (Ricklefs 1968a).

Growth of wing, tarsus, and mass was greatest between nestling days 3 and 6. The inflection point occurred at about days 8–9, when growth leveled off below adult size and mass. Studies in New York and Wisconsin indicated the Bobolink nestling mass gain inflection point occurred 8 days after hatching (Martin and Gavin 1995). Tarsus length was the closest to adult size at fledging of the three variables measured. This accelerated growth of a specific nestling characteristic may be a reflection of the selective pressure to enable young to run from the nest by day 7 if disturbed (Martin and Gavin 1995). Eastern Meadowlarks and Savannah Sparrows also attain near-adult tarsus length at fledging and are known to escape from nests by running prior to fledging (Lanyon 1995, Wheelwright and Rising 2008). Incomplete growth prior to fledging is associated with provisioning by parents after the young leave the nest, when they complete their growth to adult size (Martin and Gavin 1995).

This is the first report of linear nestling measurements, as well as the first comparison of egg size and within-clutch variation with clutch size and initiation date for Bobolinks. This study provides baseline data for future studies, as well as information on timing of critical growth for nestlings, which should prove useful for conservation and management planning for this declining grassland species.

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BREEDING PHENOLOGY AND NESTING SUCCESS OF THE YUCATAN WREN IN THE YUCATAN PENINSULA, MEXICO

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ABSTRACT.—The Yucatan Wren (*Campylorhynchus yucatanicus*) is a highly restricted endemic species inhabiting the coastal scrub at the northern portion of the Yucatan Peninsula. We describe the breeding phenology and nesting success of this endangered species from April to September 2007 for a population at Ria Celestun Biosphere Reserve. We found 232 nests of which only 110 (47%) were active at either incubation or nestling stages. Yucatan wrens initiated nest building in late April, but clutch initiation occurred in early June and lasted until the end of July, resulting in a breeding season of 2 months. Nests were exclusively in coastal scrub and the transition between coastal scrub and black mangrove (*Avicennia germinans*) forest. Eleven species of trees were used as nesting substrate, but three included 75% of all nests found. Clutch size ($\bar{x} \pm$ SD) was 3 ± 1.5 eggs with incubation and nestling periods averaging 16 ± 1.0 days, and 16.5 ± 1.9 days, respectively. Mayfield estimates of daily survival rate for incubation and nestling periods were 0.968 ± 0.005 and 0.975 ± 0.005, respectively with nesting success of 46%. The average number of fledglings per successful nest was 2.5 ± 1.3. Predation was the main cause of nest mortality accounting for 54% of the active nests. Parental care was provided by both parents, but participation of a third individual feeding nestlings was recorded at three nests, providing evidence for occasional cooperative breeding. Increasing human development in the coastal region of the Yucatan Peninsula may represent a serious threat to conservation of the Yucatan Wren due to habitat restriction and high dependency on three species of trees as nesting substrate. *Received 3 December 2008. Accepted 4 February 2010.*

Information on life history traits and social systems is scarce or lacking for many species of birds, especially those at tropical latitudes (Martin 1996, 2004). Estimation of productivity is one of the most important demographic parameters necessary to describe numerical fluctuations in space and time (Donovan et al. 1995, Jehle et al. 2004, Powell and Knutson 2006). Three approaches have been suggested to measure bird productivity: (1) percentage of nests constructed by females per year (Ricklefs and Bloom 1977, Anders and Marshall 2005), (2) nesting success (based on number of nestlings from individual broods that survive until the end of the reproductive period as fledglings), and (3) estimation of reproductive success (based on number of individuals that survive and reproduce in the following reproductive cycle). Estimation of reproductive success provides information on population dynamics, and the probability of species extinction or survival. Reproductive success and proportion of nests constructed by females have been difficult to estimate due to logistical limitations of following females during one or more reproductive seasons, or as a result of not knowing the final fate of individuals in time and space, particularly once they become independent of their parents and disperse to new areas (Ricklefs and Bloom 1977). However, nests are relatively easy to monitor and provide robust data on productivity. Thus, nesting success has been frequently used to evaluate population changes in bird communities (Ricklefs and Bloom 1977, Johnson and Shaffer 1990, Knadle et al. 2001, Jehle et al. 2004, Anders and Marshall 2005, Powell and Knutson 2006).

Researchers can monitor nests to estimate nesting success and factors that influence reproductive success including vegetation structure, depredation, nest parasitism, and climatic conditions (Hazler 2004, Martin et al. 2006). This information is essential in understanding the ecology of species, which can suggest strategies for habitat conservation and management (Peterson et al. 1993).

The Yucatan Wren (*Campylorhynchus yucatanicus*) occurs exclusively in the coastal portion of the Yucatan Peninsula in the states of Campeche and Yucatan, where it inhabits the thin line of

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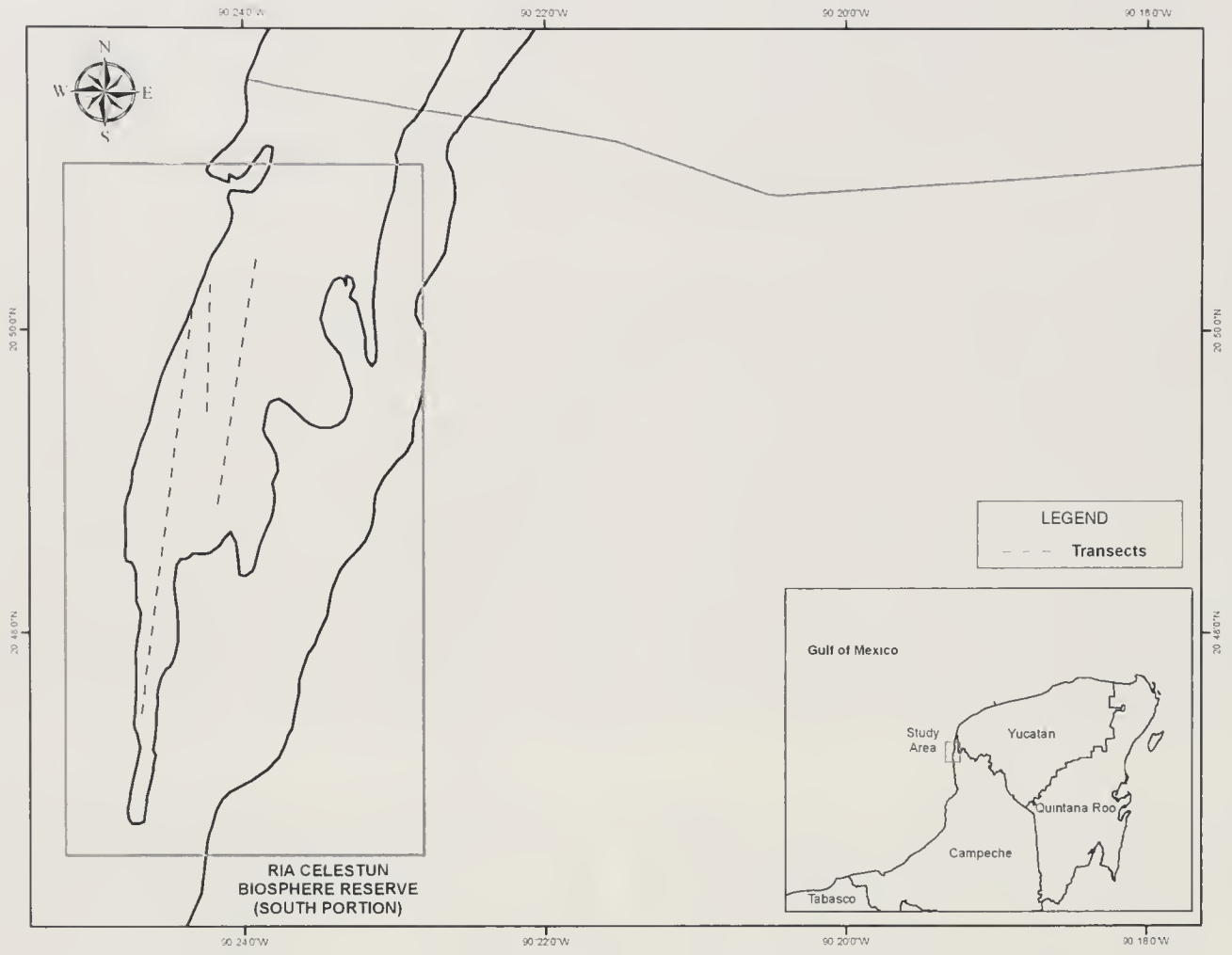

FIG. 1. Study Area showing transects at Ria Celestun Biosphere Reserve, Yucatan, Mexico.

coastal scrub (Peterson and Chalif 1989, Howell and Webb 1995, Brewer 2001). It is endemic to the Yucatan Peninsula and considered by the Mexican Government as threatened and is included on the IUCN red list as near threatened (Diario Oficial de la Federación 2002, BirdLife International 2008).

Information on the biology of this species has been limited to general descriptions of distribution and habitat use, and is largely anecdotal based on observations by Zimmerman (1957), who provided a brief description of the nest and behavior of individuals from a population at Sisal, Yucatan. Our objectives were to obtain information on (1) breeding seasonality, (2) length of incubation and brooding periods, (3) clutch size, (4) parental care, and (5) nesting success.

METHODS

Study Area.—The study was conducted during April to September 2007 at Ria Celestun Biosphere Reserve at the northwestern portion of the Yucatan Peninsula, Mexico (20° 46′ and 21° 06′ N, 90° 11′ and 90° 25′ W) on the boundaries of the states of Campeche and Yucatan (Fig. 1). The climate of the area is warm semi-dry with rain occurring mainly during summer. Annual precipitation averages 750 mm with a dry season occurring from December to May and a wet season from June to November. The mean annual temperature is 26.5° C with May being the warmest month (average 29° C) (CONANP 2000).

The most abundant types of vegetation at Ria Celestun Biosphere Reserve are coastal scrub, and mangrove and flooded lowland forests (CONANP 2000). Coastal scrub has two phases of development with the first adjacent to the beach and integrated by clumps of shrubs where the main species are bay cedar (*Suriana maritima*) and sea rosemary (*Tournefortia gnaphalodes*). The second corresponds to scrub towards the interior of the dunes in a zone where the sand is less altered and canopy height ranges from 3 to 5 m. The most common plant species in this zone are white tree (*Bravaisia berlanderiana*), wood luck seed (*Thevetia gaumeri*), sea grape (*Coccoloba uvifera*), geiger tree (*Cordia sebestena*), black poison wood (*Metopium brownie*), peccary tree (*Sideroxylon*

americanum), joewood (*Jacquinia aurantiaca*), peccary wood (*Caesalpinia vesicaria*), blackbead (*Pithecellobium keyense*), wild sage (*Lantana involucrata*), blacktorch (*Erithalis fruticosa*), mexican cotton (*Gossypium hirsutum*), and century plant (*Agave angustifolia*).

Mangrove forest is abundant along the estuary and is represented by red (*Rhizophora mangle*), black (*Avicennia germinans*), and white mangrove (*Laguncularia racemosa*) with tree heights ranging from 12 to 14 m. Other species such as pickleweed (*Batis maritima*) and sea purslane (*Sesuvium portulacastrum*) together with numerous species of grasses (Cyperaceae and Gramineae) also occur along drainage channels forming patches, characterized by short trees ranging from 1.5 to 3 m in height, known as logwood patches.

The flooded lowland forest merges between the coastal scrub and mangrove forest and is represented by logwood tree (*Haematoxylum campechianum*), milk tree (*Cameraria latifolia*), black poison wood, chicle tree (*Manilkara zapota*), gambo limbo (*Bursera simaruba*), nance (*Byrsonima crassifolia*), black olive tree (*Bucida buceras*), ceiba tree (*Ceiba aesculifolia*), buttercup tree (*Cochlospermum vitifolium*), and button mangrove (*Conocarpus erectus*).

Nest Searching and Monitoring.—We established line transects ranging from 4 to 6 km in length in each of the three main vegetation types within the study area. We visited each transect starting in April 2007 to locate wrens and nesting sites based on presence of old nests. Other wren species are known to maintain year-round nests, apparently used as dorms (Robinson et al. 2000, Yáber and Rabenold 2002). Yucatan Wrens are no exception, as old nests were found along each transect; old nests were used as evidence of wren presence and potential nesting sites. Each site was checked for nesting activity every third day with observations throughout morning (0630–1200 hrs EDT) and afternoon (1600–1930 hrs), following Martin and Geupel (1993). We found new nests, primarily by scanning trees along transects (Yucatan Wrens make nests of grasses and the yellow material contrasts with the dark background of trees used as nesting substrate). We also used parental behavioral cues including observation of birds carrying nesting material, alarm calls of wrens during both incubation and brooding, and parents delivering food to nestlings (Ralph et al. 1996). Few nests were found by accidentally flushing adults from the nest while walking. We recorded the number of nests found in each vegetation type and identified the species of trees used as nesting substrate.

We checked nests every 2–4 days until failure or success to estimate clutch initiation, length of incubation and brooding periods, and final nest fate. We monitored nests daily when a transition, hatching or fledging, was anticipated. Yucatan Wren nests are dome shaped and bulky with a tubular entrance; we used a fiberscope (Provision model 960, Chicago Miniature Inc., Hackensack, NJ, USA.) to examine nest contents and avoid damage to nests and contents. We considered a nest failed if all eggs or nestlings disappeared and successful if one or more young fledged.

We used three video cameras (SONY DCR-HC30/HC40) to record parental care and to document cooperative breeding as this behavior has been reported for other species of wrens (Rabenold 1984), Cameras were used at 45 of 110 active nests for a total of 200 hrs of video recording. Video cameras were used only at nests with nestlings. Each video was later reviewed with the aid of a TV monitor to calculate parental visitation rate, feeding, and presence of individuals other than the parental pair.

Statistical Analyses.—We report means ± SD for all variables unless otherwise specified. Nesting success and daily nest survival probabilities were calculated following Mayfield (1961, 1975).

RESULTS

Timing of Breeding.—We found 232 nests throughout the 2007 breeding season of which 110 (47%) were active: laying (59), incubation (40), and nestling (11). The remaining 122 (53%) nests were abandoned during the building stage. Yucatan Wrens started nest building in early April, but most nests were built in June (50%) with fewer in May (35%), July (13.5%), and April (1.3%). Nests were build by both parents and the average time to build a nest was 6 ± 1.5 days (range 4–8, n = 149). Clutch initiation started in June despite early nest building. The earliest clutch recorded was on 11 June and the latest on 28 July; the breeding season extended for 2 months (Jun–Jul). There was a time lag of 19 ± 8.5 days (range 5–33, n = 24) between the end of nest building and laying of the first eggs. Old nests within territories were not used for breeding.

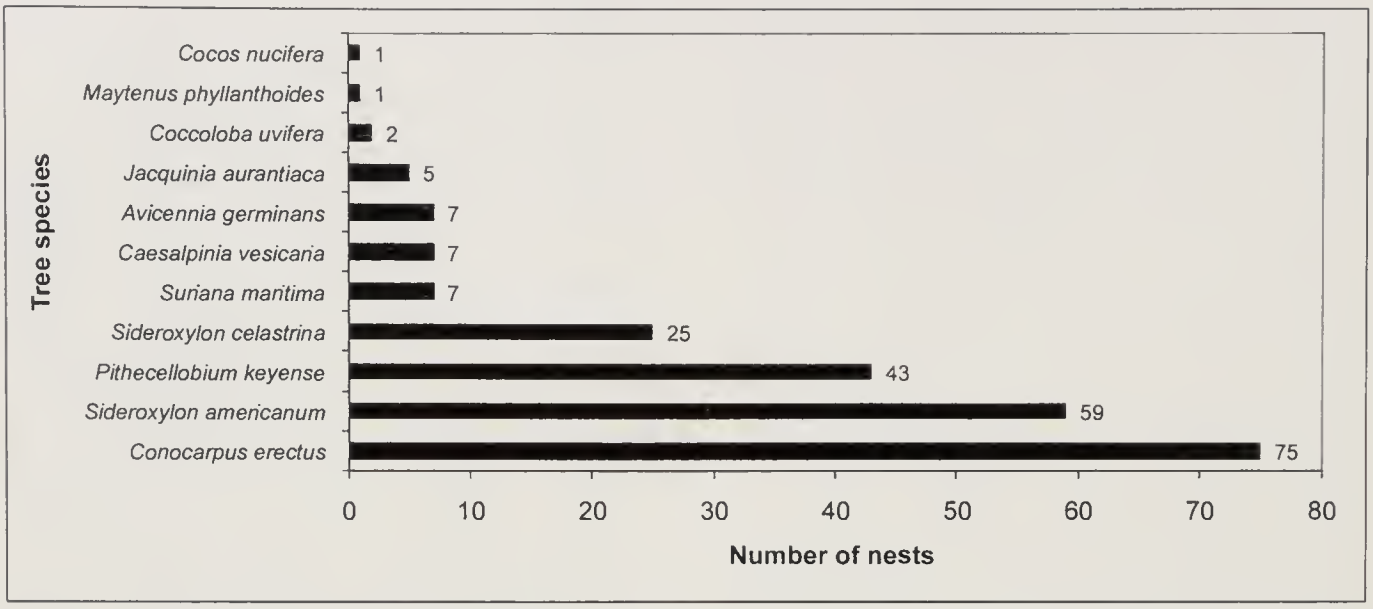

FIG. 2. Tree species used by Yucatan Wrens as nesting substrate at Ria Celestun Biosphere Reserve, Yucatan, Mexico.

Clutch Size, Length of Incubation and Nestling Periods.—Clutch size averaged 3 ± 1.5 eggs (range 1–5; n = 99 nests), but half of the nests (49.5%) had four eggs. The proportion of nests with one egg was 10.1%, two eggs = 18.2%, three eggs = 21.2%, and five eggs = 1%. Yucatan Wrens typically laid one egg per day and females initiated incubation with laying of the last egg. The incubation period averaged 16 ± 1.0 days (range 15–17, n = 47). The earliest hatching date was 28 June and the latest was 11 August. Hatching was synchronous as all eggs within individual broods hatched within 24 hrs after the first egg hatched.

Yucatan Wren nestlings fledged on average 16.5 ± 1.9 days after hatching (range 14–19; n = 51). The average number of young fledged per successful nest was 2.5 ± 1.3 (1–4 young; n = 51). The earliest date of fledging was 14 July and the latest was 23 August.

Parental Care.—Incubation feeding by Yucatan Wrens was not observed. Both parents fed nestlings at all nests observed (n = 51) for parental care. The average number of provisioning visits/hr by both parents combined was 7 ± 1.6 (range 5–9 visits). We recorded the presence of a third adult feeding young at three nests, confirming occasional cooperative breeding in this species. Fledglings remained close to the nesting site for 2–3 days after fledging and both parents continued providing care to fledglings, independently of number.

Nesting Success.—The Mayfield estimate of daily survival for the incubation period was 0.968 ± 0.005 and 0.975 ± 0.005 for the nestling period. Estimated nesting success was 46%. Nest predation was the only cause of nesting failure, accounting for loss of 54% of all active nests. We found no evidence of brood parasitism by cowbirds of Yucatan Wren nests. Ectoparasites (Diptera: Muscidae) were observed on 20 juveniles in seven nests, but no mortality was related to parasitism.

Habitat Use and Nesting Substrate.—One hundred and fifty of the 232 nests (65%) were in coastal scrub, while the remaining 82 (35%) were in flooded lowland forest (between the coastal scrub and mangrove forest). Yucatan Wrens used 11 species of trees as nesting substrate (Fig. 2). However, only three species, button mangrove, peccary tree, and blackbead supported 75% of all nests found (Fig. 2).

DISCUSSION

The breeding season of Yucatan Wrens at Celestun was highly seasonal, occurring over a period of ~ 3 months (May–Jul). Nest building started during the dry season in late April, but clutch initiation was not recorded until June suggesting initiation of breeding is closely related to seasonal occurrence of rainfall. Previous studies on avian breeding phenology have suggested that onset of breeding of tropical birds is closely connected with rainy seasons (Ahumada 2001, Tarraoux and McNeil 2003). It is possible that rainfall may also be a primary stimulus for reproductive activity for Yucatan Wrens. We did not measure the rainfall regime for the study period, but Salgado-Ortiz et al. (2008) reported that 75% of the rain occurs from June to

September in Celestun with a monthly maximum in September. Our observations of a time lag that averaged 20 days from the end of nest building to laying of the first egg in June supports the possibility that Yucatan Wrens may be using rain as an environmental cue to adjust timing of breeding.

Clutch initiation of Yucatan Wrens extended over 2 months (Jun–Jul) with no evidence of second nesting attempts after either failure or success. The clutch initiation period is similar to that recorded for Cactus Wrens (*Campylorhynchus brunneicapillus*) in Arizona (Simons and Martin 1990), but shorter than that of Stripe-backed Wrens (*C. nuchalis*) in Venezuela (Piper 1994). The difference in duration (2 months) of the breeding season between Yucatan and Striped-backed wrens may be explained by seasonal effects occurring in the flooded savanna where the latter species occurs. The savanna remains relatively wet weeks after arrival of the first rains, presumably resulting in food being available for a longer period, which in turn ensures the possibility of more nesting attempts.

The average clutch size of Yucatan Wrens was three eggs, similar to that of Rufous-naped Wrens (*C. rufinucha*) in Costa Rica (Skutch 1985), and slightly smaller than that of Cactus Wrens (4 eggs) in Arizona (Simons and Simons 1990). The smaller clutch size of the Yucatan Wren appears to fit the latitudinal trend in clutch size from temperate to tropical latitudes. However, the evidence is inconclusive because ~ 50% of Yucatan Wren nests had four eggs suggesting differences in clutch size may not be significant, as has been found for open cup nesting species (Martin 1996).

The incubation period averaged 16 days, similar to that of the Cactus Wren; however, incubation started with the laying of the last egg by Yucatan Wrens in contrast to the first egg for Cactus Wrens (Farley and Stuart 1994). It is possible Yucatan Wrens begin incubation with the last egg to synchronize hatching. We observed that hatching of all eggs occurred within 24 hrs of hatching of the first egg, but were unable to obtain detailed description of hatching synchrony. The difference in initiation of incubation versus that of Cactus Wrens could be attributed to the large change of temperatures throughout the day occurring in the arid desert where Cactus Wrens occur (Mezquida 2004). Cactus Wrens starts breeding in March (Simons and Martin 1990), coinciding with frequent cold fronts from the north resulting in extreme weather conditions. Initiation of incubation with laying of the first egg could be a local adaptation to protect eggs from unstable weather conditions (Hansell 2000).

Parental care, as confirmed by video cameras, was provided by both parents and an occasional adult helper at three nests. We were not able to capture and color-band individuals, but videotaping provided evidence of individuals in addition to the parents visiting active nests and providing food to nestlings. We suspect that cooperative breeding its more widespread in Yucatan Wrens, but confirmation requires study with color-banded individuals. Austad and Rabenold (1986) and Rabenold (1990) reported cooperative breeding has been documented in nine of the 13 species of *Campylorhynchus*, not including the Yucatan Wren. Our evidence is scarce, but the highly restricted coastal arid scrub where the Yucatan Wren occurs and dramatic seasonal changes have been suggested as environmental or causative factors for occurrence of cooperative breeding in other species (Rabenold 1990).

Predation was the main cause of failure of Yucatan Wren nests. Stutchbury and Morton (2001) report nest depredation rates for tropical birds as a group are higher (65–80%) compared to those of temperate zone birds. The nest loss (54%) for Yucatan Wrens at Celestun is less than reported as typical for tropical birds. Nest depredation has been reported to generally be higher for open cup nests that for closed nests (Collias and Collias 1984, Martin 1995, Auer et al. 2007). Lower nest depredation of Yucatan Wrens could be a result of the dome-shaped nest. Clumping of nests has been reported to reduce the probability of depredation, increasing reproductive success (Bowman and Harris 1980, Martin 1993). Yucatan Wrens built several nests in the same tree; we did not study the direct effect of clumped nests on nesting success, but this behavior could explain the lower depredation rate of Yucatan Wren nests compared to Mangrove Warblers (*Dendroica petechia bryanti*) nesting in the same area (67–88%) (Salgado-Ortiz et al. 2008). The Mayfield estimate of daily survival rate of Yucatan Wren nests (0.978) was higher than reported for Mangrove Warblers (0.950) in the same area (Salgado-Ortiz et al. 2008), but was similar to that reported for Cactus Wrens (0.99) (Ricklefs 1968). Daily survival rates of Yucatan

and Cactus wrens provide evidence to support the hypothesis that dome-shaped nests survive better than open cup nests (Martin 1996).

Construction of several nests in clumps appears to be widespread behavior among the Troglodytidae (Márquez-Valdelamar 1998). Nests built, but not intended for breeding are used as ''dummy'' nests, a strategy suggested to reduce depredation and increase chances of adult survival (Márquez-Valdelamar 1998, Robinson et al. 2000, Puga-Vazquez 2008). Robinson et al. (2000) demonstrated that only half of the nests constructed by Song Wrens (*Cyphorhinus phaeocephalus*) in Panama were used for reproduction, while the others were constructed to confuse nest predators. Yucatan Wrens used 47% of the total new nests found over the breeding season. Some nests in our study were destroyed during the building stage by other individuals of the same species or unidentified predators, while others were finished, but remained unused for reproduction, supporting the ''dummy'' anti-predator strategy.

Yucatan Wrens nested exclusively within coastal scrub and the transition to mangrove forest. This vegetation zone extends < 1 km inland. Yucatan Wrens mostly used three species of trees with button mangrove being used as the main nesting substrate. This indicates Yucatan Wrens are highly dependent on this tree species as nesting substrate. Previous studies have shown that other species of Troglodytidae construct nests mainly in trees with thorns, particularly of the genus *Acacia*. It has been hypothesized that use of thorny plants as nesting substrate is for protection from predators (Young et al. 1990, Márquez-Valdelamar 1998, Skutch 2001). This also has been suggested for Cactus Wren, which uses cactus (*Opuntia* spp.) as nesting substrate (Facemire et al. 1990). Yucatan Wrens at Celestún used species lacking thorns, despite several thorny species occurring in coastal scrub. We believe the high use of button mangrove as nesting substrate reflects the greater abundance of this tree species within the preferred nesting habitat. Yucatan Wrens were not locally rare in our study area, but are highly habitat restricted and show marked preference in nesting substrate. Button mangrove is widely used as firewood by local people who are reducing the availability of this species. This use may have negative implications on future nesting success of Yucatan Wrens. The current human population increase and increasing land development resulting from the tourist industry in coastal areas are becoming serious threats to future conservation of Yucatan Wrens and their habitat.

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BREEDING BIOLOGY AND NATURAL HISTORY OF THE SLATE-THROATED WHITESTART IN VENEZUELA

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ABSTRACT.—We provide details on the breeding biology of the Slate-throated Whitestart (*Myioborus miniatus*) from 126 nests found during seven breeding seasons, 2002–2008, at Yacambú National Park, Venezuela. Nesting activity peaked in late April and May. Only the female built the nest and incubated the eggs. Males rarely visited the nest during these stages. Mean clutch size (2.1 ± 0.04 eggs, $n = 93$) was the smallest recorded for the Slate-throated Whitestart. Incubation and nestling period lengths were 15.3 ± 0.31 ($n = 21$) and 10.8 ± 0.24 ($n = 7$) days, respectively. Attentiveness (% of time on the nest) during incubation (59 ± 1.6%, $n = 52$) was similar to other tropical warblers and much lower than northern relatives. This caused a relatively low egg temperature (34.40 ± 0.33° C, $n = 6$ nests, 20 days) compared with north temperate birds. Both parents fed nestlings and increased their provisioning rates with nestling age. Growth rate based on nestling mass ($k = 0.521 \pm 0.015$) was faster than for other tropical passerines but slower than northern relatives. Predation was the main cause of nesting failure and rate of predation increased with age of the nest. An estimated 15% of nests were successful based on an overall Mayfield daily predation rate of 0.053 ± 0.007. This study confirms a strong latitudinal variation in life history traits of warblers. *Received 17 September 2009. Accepted 12 March 2010.*

New World wood warblers (Parulidae) are a small-sized and mostly insectivorous group of birds. Much work has been done on north temperate species, but resident tropical warblers are relatively poorly studied (but see Skutch 1945, 1954; Greeney et al. 2008; Cox and Martin 2009; Morales-Rozo et al. 2009). One of the most broadly distributed genera of this family is *Myioborus*, which consists of 12 species (Sibley and Monroe 1990, Curson et al. 1994, Ridgely and Tudor 1994). The most widespread species of the genus is the Slate-throated Whitestart (*M. miniatus*) which is a resident of mountain ranges between 700 and 2,500 m elevation in humid and wet forests (Ridgely and Tudor 1994). It occurs from Mexico to southern Bolivia, and unconfirmed data extend its distribution to northern Argentina (Di Giacomo 1995). It also is vagrant in southern Arizona, New Mexico, and west Texas (Dunn and Garrett 1997). However, the most northern breeding record is in the Sierra Madre Oriental, Mexico (McCormack et al. 2005).

Slate-throated Whitestart populations are not threatened anywhere within their range and tolerate nesting in disturbed areas (Collins and Ryan 1994, Curson et al. 1994, Mumme 2010). For these reasons, the species is evaluated as one of Least Concern (IUCN 2009).

The wide distribution of this species, which is almost equal to that of the entire genus, makes the Slate-throated Whitestart an interesting species for examining geographical variation. The Slate-throated Whitestart has great plumage and genetic variability along its range (Pérez–Emán 2005). The 12 subspecies recognized show a cline in belly colors from red to orange and yellow from North to Central and South America (Curson et al. 1994). Yet, intraspecific and interspecific comparisons in life-history traits of *Myioborus* are scarce (Skutch 1945, 1954; Collins and Ryan 1994; Mumme 2010).

M. m. ballux is the most common race in the Andes of Venezuela, Colombia, and part of Ecuador. Genetic information for our study site (Yacambú National Park, Venezuela) is lacking, but geographical proximity to Cubiro as well as the occurrence of some slight orange in the breast suggests *M. m. ballux* is also the race occurring in Yacambú (Phelps and Phelps 1950; J. L. Pérez-Emán, pers. comm.).

Our objective is to provide new information on the breeding biology of the Slate-throated Whitestart in a montane forest in northwest Venezuela. We compare our results with life-history traits recorded for other warblers, especially other *Myioborus* species.

METHODS

Study Area.—This study was conducted during seven consecutive breeding seasons, from early March to early July in 2002 to 2008 at Yacambú

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National Park (09° 42′ N, 69° 42′ W) in Lara State, Venezuela. This is a montane forest consisting mainly of primary forest in the northern part of the Andes. The park ranges from 500 to 2,200 m, but our study plots were restricted to 1,350–2,000 m elevation (Fierro-Calderón and Martin 2007). The rainy season spans from mid-April to mid-July with a peak from May to June.

Field Procedures.—Slate-throated Whitestart nests were found almost solely by observing parental behavior, especially during nest building when it is easiest to find them (Martin and Geupel 1993). Nests were checked every other day, except at stage-changing events (hatching or fledging), when they were checked every day or twice per day. Nest size was measured using a ruler with an accuracy of 0.01 cm for outer diameter (from edge to edge of nest) and height (exterior bottom-to-top of nest), and inner diameter (from edge to edge of cup) and height (bottom-to-top of cup). Eggs and nestlings were weighed with a portable electronic scale (ACCU-LAB, Elk Grove, IL, USA) with an accuracy of ±0.001 g. Mean egg mass was calculated only for eggs weighed between days 0 (last egg laid) and 2 of incubation. We measured the tarsus of nestlings using digital calipers (Mitutoyo, Kingsport, TN, USA) with an accuracy of 0.01 mm.

We videotaped nests during incubation and nestling periods in 6–8 hr sessions, starting within 30 min of sunrise (Martin and Ghalambor 1999, Fierro-Calderón and Martin 2007). This allowed us to calculate parental attentiveness (percentage of time on nest for incubating or brooding), as well as on- and off-bout duration and parental provision rates. We sought to videotape incubation in three periods to examine age-related changes in behaviors: early (2–3 days after the last egg was laid), middle (days 6–10) and late (2–3 days before average hatching date) incubation. We recorded parental behavior in two stages during the nestling period: early (day 2–3 after hatch day) and pin break (day in which the eighth pin feather broke its sheath). The latter is possible because pin feather tips turn white the day before they break. Activity recorded in videotapes as well as observation of predation events during nest checks allowed us to identify some of the predators.

We recorded egg temperatures by inserting thermisters on day 1 or 2 of the incubation period into one egg in a nest and the hole was sealed with glue (Weathers and Sullivan 1989). The wire was passed through the back of the nest and connected to a HOBO Stowaway XTI datalogger (Onset Corp., Bourne, MA, USA) that recorded temperatures every 12–24 sec for 5–7 days per nest, unless the nest was depredated earlier (Martin et al. 2007).

Statistical Analyses.—All means are reported with their standard errors (SE). Sample sizes are number of nests in all cases unless otherwise noted. Mean initiation date was calculated only for nests in which the exact egg laying date was known. Nesting season length was estimated as the number of days for the middle 90% of nests initiated (excluding the earliest and latest 5% of initiations) following Martin (2007). We calculated the incubation period as the number of days between the last egg laid and the last egg hatched (Briskie and Sealy 1990, Martin 2002). Incubation periods were only calculated for nests in which the exact day the last egg was laid and exact hatch day were known. We quantified the nestling period as the number of days between the last egg hatching and the last nestling fledging, again based only on exact observations. We used analyses of variance (ANOVA) with significance at $\alpha = 0.05$ to test changes in parental behavior during incubation and nestling stages, and used LSD *post-hoc* tests among periods. Nestling growth curves were calculated following Remeš and Martin (2002). We included measurements of mass and tarsus length for nestlings in which the exact age was known for these analyses. Mortality and survival analyses of nests were calculated considering the elapsed time of the observations to allow inclusion of nests found in different stages following Mayfield (1975). Nests that failed because of experimental activities were excluded from estimation of daily survival or mortality.

RESULTS

Nest Description.—The highest nest located was at an elevation of 1,674 ± 5 m asl; we did not see or hear any Slate-throated Whitestarts above this elevation even though we worked to 2,000 m. Nests were in small nooks on banks or slopes and often built in open or disturbed areas; including road banks or human-made trails inside the forest. However, nests were also found on slopes within undisturbed forest. Nests were highly cryptic because they were usually hidden by surrounding shrubs, ferns, or grasses. Only the female was observed going to and from the nest (mainly in

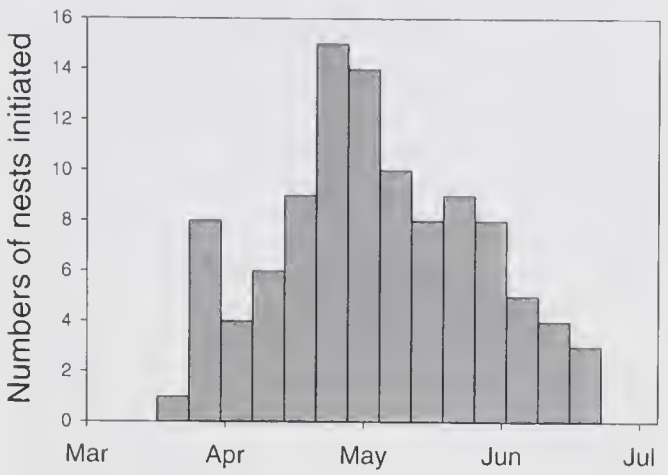

FIG. 1. Numbers of nests initiated (i.e., first egg laid) each week beginning 1 March for Slate-throated Whitestarts at Yacambú National Park, Venezuela during 2002–2008. Only nests for which initiation date was observed are included (n = 106).

morning hrs) to build the nest. The male was nearby in the surrounding trees, usually singing and hunting insects. The first nests of the season were often built over 2 to 4 weeks in a rhythm that started with several nest-building visits per day that slowly increased over time to much more active building. Nests of later attempts were built over 3 to 4 days in much more active behavior.

The nest was a dome-shaped construction entirely built with dry material including pieces of grass, several types of dry leaves, roots, and small twigs. The lining consisted of fine and soft dry fibers. The entrance was circular to elliptical (wider than higher). Nest orientation at 73 nests spanned from 1 to 334° with no orientation preferences. The internal dimensions of the cup averaged 49.1 ± 4.7 mm in diameter and 31.4 ± 9.5 mm in height (n = 66). The outer dimensions of the nest averaged 103.9 ± 21.2 mm and 64.8 ± 25.0 mm for diameter and height, respectively.

Nesting Chronology.—The nesting period of Slate-throated Whitestarts in Yacambú spanned from late March to late June based on 126 nests over seven breeding seasons. The earliest and latest nests across all years of study were initiated on 26 March and 23 June, respectively. Both nests were found before the first egg was laid, yielding precise documentation of these extremes, but even back-calculating nests that were already initiated when found did not exceed these extremes. The mean initiation date was 7 May (± 2.2 days, n = 106) and highest nesting activity occurred at the end of April and through May (Fig. 1).

Re-nesting activities were observed within 6–8 days after a nest failed and within a 15-m radius of the previous nest (n = 10). Banded individuals allowed confirmation that it was a re-nesting attempt by a particular pair of individuals. The nesting season of the Slate-throated Whitestart in Yacambú was 77 days, but this species appears to be single brooded; we did not observe any breeding activity of the same pair in the same season after a successful brood.

Clutch Size and Eggs.—Mean clutch size for the Slate-throated Whitestart was 2.1 ± 0.04 eggs (n = 93). We recorded one instance of a single egg clutch (1%), 15 nests had three eggs (16%), and the rest had two eggs (83%). Three-egg clutches did not exceed 25% of the clutches in any year, but three-egg clutches were observed in all years except 2004 (n = 14 in 2004).

Eggs were laid on consecutive days and generally early in the morning (i.e., before 0800 hrs). The eggs were elliptical to sub-elliptical and the shell was dull white with irregularly distributed dark red to brown spots. Mean egg mass was 1.61 ± 0.01 g (n = 152 eggs) and ranged from 1.20 to 1.94 g. The mean egg mass represented 19% of adult female body mass (10.1 ± 0.15 g, n = 20 females).

Incubation Period.—Incubation began when the last egg was laid, but nest attentiveness was highly variable on that day. Eggs hatched synchronously in all cases. Only the female incubated, and the male rarely visited the nest to feed the female. The male did not visit during 6–8 hrs of video observations at 31 of 52 nests sampled during incubation. Overall, the male averaged 0.11 ± 0.02 trips/hr to the nest (n = 52) during incubation.

The incubation period of the Slate-throated Whitestart averaged 15.3 ± 0.31 days (n = 21) varying from 14 to 18 days. Overall, nest attentiveness (percent of time spent on the nest incubating) during this stage averaged 59 ± 1.6% (n = 52). Nest attentiveness increased ($F_{2,49}$ = 15.8, $P < 0.001$) from early incubation to mid-incubation but did not continue to increase in late incubation (Fig. 2A). The increase in nest attentiveness was caused by reduction in duration of off-bouts with increasing age of the embryo (Fig. 2B; $F_{2,49}$ = 5.4, P = 0.008). Duration of on-bouts did not change ($F_{2,49}$ = 1.49, P = 0.17) with age of the embryo (Fig. 2B). On- and off-bouts averaged 33.4 ± 1.63 min and 22.8 ± 2.65 min (n = 52 in both cases), respectively. Temperature of Slate-throated Whitestart eggs averaged 34.40 ± 0.33 C over 24-hr periods (n =

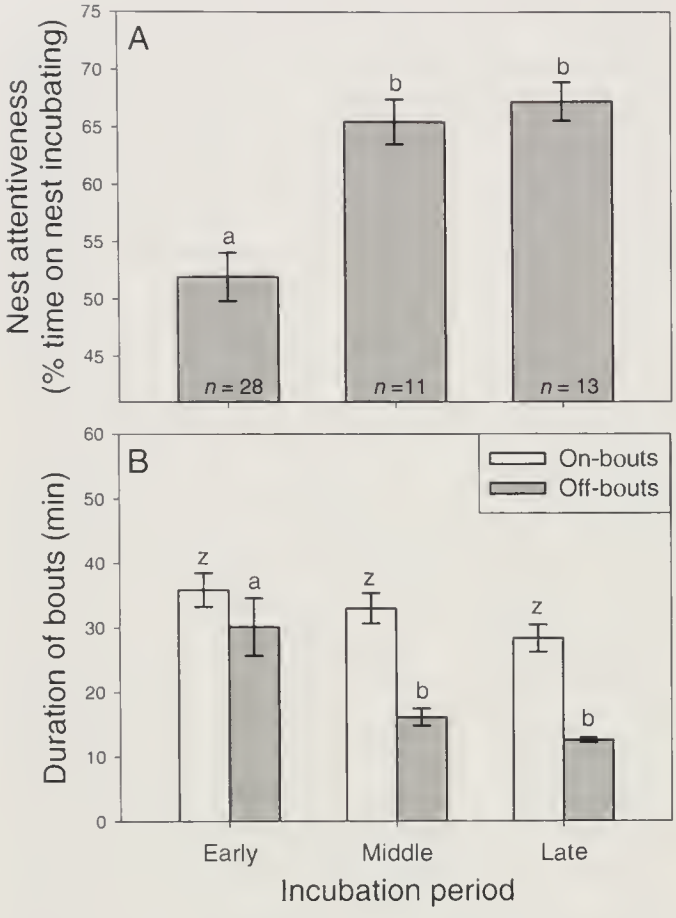

FIG. 2. Mean ± SE for (A) nest attentiveness, and (B) on- and off-bout durations across three periods of incubation: early (days 1–5), middle (days 6–10), and late (days 11–17) for Slate-throated Whitestarts at Yacambú National Park, Venezuela. Sample sizes reflect numbers of nests. Different letters among periods indicate significant differences ($\alpha = 0.05$) based on LSD tests of each bout type (on- vs. off-bouts) separately.

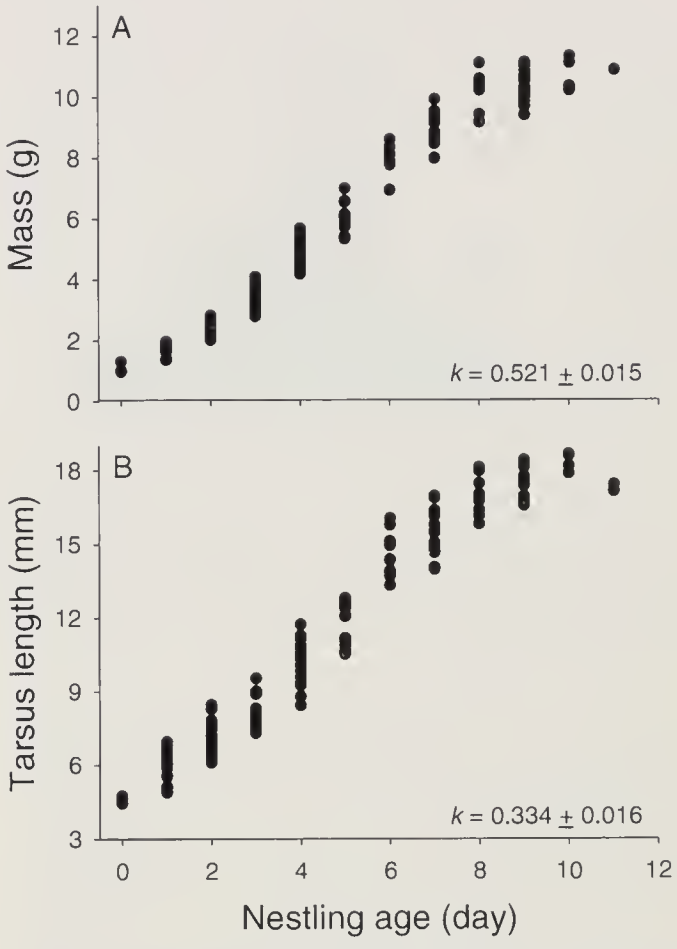

FIG. 3. (A) Mass and (B) tarsus length measurements of Slate-throated Whitestart nestlings at Yacambú National Park, Venezuela plotted against age. Growth rate constant (k) is indicated in each graph.

6 nests, 20 days of sampling) based on an overall mean taken from the means of each nest.

Nestling Period.—Hatchlings had sparse natal down with pink-orange skin, and were blind. The eighth primary feather broke its sheath on days 6 or 7. Brooding attentiveness was by females alone and averaged 63 ± 2.9% (n = 10) at the beginning of the nestling period (days 0–3 of age) and decreased dramatically ($F_{1,15} = 92.6$, $P < 0.001$) to 11 ± 4.9% (n = 7) at pin break. Both females and males provisioned the nestlings at an average rate of 3.77 ± 0.44 trips/hr (n = 10) early in the nestling period (days 0–3), but provisioning rate markedly increased ($F_{1,15} = 25.7$, $P < 0.001$) to 9.41 ± 1.18 trips/hr (n = 7) at pin break.

Nestlings fledged in 10.8 ± 0.24 days (n = 7) after hatching, ranging from 10 to 11.5 days. Growth rate based on nestling mass (Fig. 3A) was greater than when based on tarsus length (Fig. 3B). Nestling weights on the last 2 days in the nest (days 10 and 11) averaged 10.78 ± 0.22 g (n = 5 fledglings) compared with mean adult mass (10.1 ± 0.15 g for the female [n = 20] and 10.1 ± 0.11 g for the male [n = 36]).

Nest Survival.—Eighteen of 126 nests were excluded from nest survival analyses because of disruption by experimental activities or because they were abandoned before egg-laying. Overall daily mortality rate for the remaining nests was 0.065 ± 0.008 (n = 108 nests; 1,084.5 exposure days) and only 15% of the nests were successful (based on a total nesting period of 30.2 days). Overall daily nest predation rate was 0.053 ± 0.007. Daily nest predation rates increased with age of the nest from 0.037 ± 0.021 (n = 81.5 exposure days) during egg-laying to 0.052 ± 0.008 (n = 736 exposure days) during incubation to 0.060 ± 0.015 (n = 267.0 exposure days) during the nestling stage. Predators included mostly birds (e.g., small raptors, jays, and woodwrens) but also small mammals (e.g., squirrels and tayra [*Eira barbara*]).

DISCUSSION

The nesting season for Slate-throated Whitestart in Yacambú (late Mar to late Jun) was almost identical to reports elsewhere in Venezuela (Collins and Ryan 1994), and Costa Rica (Skutch 1954, Mumme 2010). In general, the highly seasonal breeding activity began at the end of the dry season and continued through the rainy season.

Behavior during nest building was consistent with previous observations reported by Skutch (1945, 1954) and Mumme (2010) in Central America, and for other *Myioborus* species (e.g., *M. pictus* [Marshall and Balda 1974] and *M. flavivertex* [Morales-Rozo 2009]). Characteristics of Slate-throated Whitestart nests appear to be highly conservative along the broad range of the species. Slate-throated Whitestart nests in Yacambú were in the same types of places reported from Central America (Skutch 1954, McCormack et al. 2005, Mumme 2010) and Venezuela (Ewert 1975, Collins and Ryan 1994). Slate-throated Whitestart nests were quite similar to some other members of the genus, including *M. melanocephalus* (Greeney et al. 2008), *M. torquatus* (Skutch 1954), *M. brunniceps* (Auer et al. 2007), and *M. flavivertex* (Morales-Rozo et al. 2009). However, some tropical *Myioborus* species, such as *M. ornatus*, apparently build open cup nests (Curson et al. 1994; O. Cortés, pers. comm.). Painted Redstart (*M. pictus*), the most northern species of the group, only occasionally builds an enclosed nest, and more often makes an open cup with the roof substituted by natural overhangs such as rocks, logs, and pine needles (Marshall and Balda 1974). Open-cup nests are common for warblers outside of the tropics. The placement of nests in small holes in the ground is also typical of some North American parulids, such as ground-nesting *Vermivora*, which do not build a roof (Martin 1993).

Clutch size for Slate-throated Whitestart at our study site was relatively constant with 83% of nests containing two eggs. The mean clutch size in Yacambú (2.1 eggs) was relatively small compared with that of *M. m. pallidiventris* only 250 km from our study site, which averaged 2.7 eggs based on six nests (Collins and Ryan 1994). This difference may reflect sample size issues, but it is notable that four of their six nests (67%) had three eggs, while only 15 of 93 nests (16%) had three eggs in our study. Moreover, we did not find more than 25% of nests with three eggs in any individual year. Other *Myioborus* species near the equator also had two-egg clutches. *M. melanocephalus* in Ecuador had two eggs in all of seven nests (Greeney et al. 2008), and *M. flavivertex* in Colombia had two eggs in the only nest observed (Morales-Rozo et al. 2009). *Basileuterus tristriatus* in Yacambú had a mean clutch size of 1.96 eggs and only one of 96 clutches had three eggs (Cox and Martin 2009). Thus, two eggs near the equator may be more typical of warblers, but the frequency of occurrence of three eggs needs further study in *Myioborus*.

Variation in clutch size among latitudes is clear. *M. m. aurantiacus* in Costa Rica usually laid three eggs with mean clutch sizes of 2.84 eggs from 13 nests (Skutch 1954) and 2.89 from 82 nests (Mumme 2010). The only nest observed for *M. m. hellmayri* in Guatemala had three eggs (Skutch 1954), *M. brunniceps* in Argentina had a mean clutch size of 2.6 eggs (Auer et al. 2007), while *M. pictus* in Arizona had a mean clutch size of 3.7 eggs (Marshall and Balda 1974). In contrast, warblers in the north temperate region typically have mean clutch sizes of 4–5 eggs (Martin 1988). Thus, tropical warblers have a strong reduction in clutch size compared to north temperate warblers, but variation within the tropics and subtropics both in Slate-throated Whitestart races and among congeners also appears evident.

Incubation behavior and duration (15.3 days) of the Slate-throated Whitestart in Yacambú seem to be typical for tropical and subtropical warblers (see Cox and Martin 2009) and differ substantially from northern relatives. The mean incubation period was about a day longer than for other subspecies (Skutch 1954, Collins and Ryan 1994, Mumme 2010). However, other whitestart species and most tropical warblers have incubation periods ranging from 14 to 16 days (Martin et al. 2007, Cox and Martin 2009), and our results fit in the middle of this range. Longer incubation periods in the tropics and subtropics, compared to northern species, have been attributed to lower nest attentiveness which causes colder incubation temperatures (Martin 2002, Martin et al. 2007, Martin and Schwabl 2008, Londoño 2009). Nest attentiveness of Slate-throated Whitestarts at our study site was relatively low but similar to other tropical and southern warblers (Cox and Martin 2009). Skutch (1954) studied one nest of Slate-throated Whitestart in Guatemala during middle

incubation, and both nest attentiveness (67.4%) and duration of bouts (on-bouts = 37.6 min; off-bouts = 18.2 min) were similar to our observations for mid-incubation (Fig. 2).

Length of the nestling period (10–11 days) had low variation within Yacambú and was similar to that observed for Slate-throated Whitestarts in other localities (Skutch 1954, Collins and Ryan 1994, Mumme 2010). Nestling periods in other species of *Myioborus* are similar to Slate-throated Whitestarts (Skutch 1954, Marshall and Balda 1974, Auer et al. 2007, Greeney et al. 2008). Most warblers have a nestling period within a range of 9–13 days (Cox and Martin 2009) even when including north temperate and tropical species (Elliott 1969, Martin 1995, Remeš and Martin 2002, Martínez et al. 2004, Di Giacomo 2005, Auer et al. 2007, Cox and Martin 2009). The duration of the nestling period appears to be a more conservative life-history trait within Parulidae than incubation period.

Slate-throated Whitestarts in Costa Rica made 20.3 provisioning trips/hr, on average, during nestling ages 5–9 days (Mumme 2010), which is twice the rate that we observed (9.41 trips/hr) for this species in Yacambú on days 6–7. Despite the much higher provisioning rate, nestlings averaged the same weight on days 7–8 in both places: 9.5 g in Costa Rica (Mumme 2010) and 9.5 ± 0.17g (n = 24) in Venezuela (this study). The larger clutch size in Costa Rica (Mumme 2010) may account for the higher provisioning rate and similar nestling size compared with our site. The larger clutch size and similarly sized nestlings with higher parental provisioning rates in Costa Rica (Mumme 2010) compared with our site may suggest that food is more limiting at our site for this species.

Growth rate estimates are scarce for tropical warblers. One estimate based on limited data for the Slate-throated Whitestart in Venezuela (Collins and Ryan 1994) found that nestlings grew at a rate (k = 0.522) based on mass almost identical to our estimate from Yacambú (k = 0.521, Fig. 3). Generally, tropical passerines grow more slowly than species in temperate regions (Ricklefs 1976, Cox and Martin 2009). Our estimated growth rate (Fig. 3) was slower than estimates for north temperate warblers (i.e., Remeš and Martin 2002, Cox and Martin 2009), but faster than for many other tropical passerines (Ricklefs 1976). This relatively fast growth of nestlings given slow embryonic development (i.e., long incubation periods) demonstrates that developmental rates in embryonic and post-natal stages are not constrained by each other.

Nest design is thought to be an important factor influencing predation rate and failure from weather (Collias and Collias 1984, Auer et al. 2007). The last may be especially important in tropical and subtropical montane forests where rains during the breeding season are quite intense. Enclosed nests in these environments may afford nest contents protection from rain (Collias and Collias 1984) as well as predation (Auer et al. 2007). The daily predation rate of Slate-throated Whitestarts in Yacambú was higher than the average for all non-cavity-nesting species studied at this site (0.041 ± 0.003, n = 38 spp.; TEM, unpubl. data). This average was remarkably similar to the average for 10 non-cavity-nesting species studied in Panama (Robinson et al. 2000). Thus, the domed ground nests of this warbler in Yacambú are readily found by predators.

The Slate-throated Whitestart in Yacambú had a relatively high daily predation rate, small clutch size, long incubation period, and low nest attentiveness during incubation, typical of many tropical passerines (Skutch 1954; Martin et al. 2000, 2007; Cox and Martin 2009). Warblers appear to have strong divergences among relatives across geographic space, making them an important group for studying latitudinal changes in life-history strategies. Some traits, such as clutch size seem to have geographic variation even within the tropics within this species and genus. Other features of Slate-throated Whitestart nesting behavior, including nest construction and placement, nestling period length, and growth rate are relatively conservative. Focusing effort on parulids in tropical latitudes in particular could strengthen many aspects of life history theory.

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REPRODUCTIVE BIOLOGY OF A GRASSLAND SONGBIRD COMMUNITY IN NORTHCENTRAL MONTANA

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ABSTRACT.—Successful conservation of grassland bird populations requires basic information on their breeding biology; in particular, information from undisturbed native prairie over an extended period of time. We present data collected at Bowdoin National Wildlife Refuge in northcentral Montana on the reproductive biology of six grassland bird species that breed in mixed-grass prairie: Sprague's Pipit (*Anthus spragueii*), Savannah (*Passerculus sandwichensis*), Grasshopper (*Ammodramus savannarum*), and Baird's (*A. bairdii*) sparrows, Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). Basic measures of reproductive biology are presented, including estimates of nest density, phenology, fecundity, parasitism rates, and nest success, and how these and other characteristics varied across years. Nests (n = 1,494) of the six focal species accounted for 98% of all passerine nests found during 1997–2007; Chestnut-collared Longspurs (51%) were the dominant breeding species. Total nest density across years ranged from 20 to 41 nests per 40 ha (CV = 26%) on unburned sites. Mean clutch initiation date and clutch size varied little across years; however, clutch size tended to decrease over the course of a season, regardless of bird species. Daily nest survival rates did not differ markedly among bird species, but did vary substantially among years, suggesting that year-dependent factors were affecting nest success among all species similarly. *Received 20 December 2008. Accepted 28 February 2010.*

Declines in grassland bird populations have been consistently greater and geographically more widespread than in any other avifaunal group in North America (Knopf 1996, Askins et al. 2007, Sauer et al. 2008), which has been particularly evident for breeding endemics of the northern mixed-grass prairie (Knopf 1996). This has been attributed to many factors, including habitat conversion and fragmentation (Askins et al. 2007), woody vegetation encroachment (Houston and Schmutz 1999), removal of native grazers (Knopf 1994, 1996) and fire (Higgins 1984), and increased predation and parasitism (Basore et al. 1986, Davis and Sealy 2000).

Conservation of grassland bird populations requires basic information on their breeding biology, especially data from undisturbed native prairie over an extended period of time. Large expansive areas of shortgrass and mixed-grass prairies still exist in the western portion of the Great Plains, including northcentral Montana, where these grasslands are relatively intact. In addition, northern prairie grasslands are fundamentally dynamic. Local temporal variability in grassland conditions are largely a function of weather, which can influence plant community structure and composition, both within- and between seasons (Igl and Johnson 1999, Winter et al. 2005, Askins et al. 2007). Fluctuations in habitat conditions result in notable shifts in local bird population densities (Igl and Johnson 1999, Winter et al. 2005) as many native grassland bird species adapt to shifting habitat conditions with nomadic behavior (Clark and Shutler 1999, Ahlering and Johnson 2006, Jones et al. 2007). Consequently, long-term studies focusing on the same population can be instrumental to understanding how reproductive characteristics vary over time.

We studied six species, two of which, Sprague's Pipit (*Anthus spragueii*) and Baird's Sparrow (*Ammodramus bairdii*) are breeding endemics to the northern mixed-grass prairie, and a third, Chestnut-collared Longspur (*Calcarius ornatus*), breeds only in the short to mixed-grass prairie of the western and northern Great Plains. These species have been the subject of recent studies on their reproductive biology (Davis and Sealy 1998, Winter 1999, Davis 2003), and on habitat and management effects (Madden et al. 1999, Davis 2005). However, few studies have occurred in Montana (Hill and Gould 1997, Robbins and Dale 1999, Green et al. 2002), or over an extended period of years. Savannah (*Passerculus sandwichensis*), and Grasshopper (*Ammodramus savannarum*) sparrows, and Western Meadowlarks (*Sturnella neglecta*) have been well-studied

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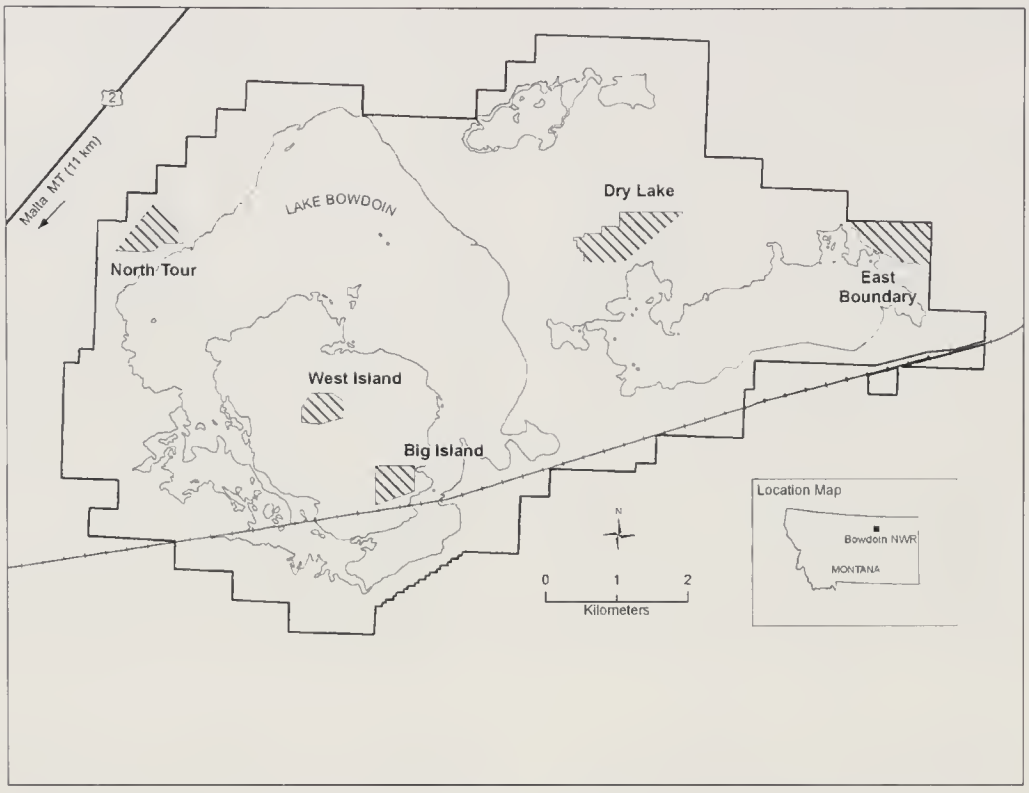

FIG. 1. Study sites at Bowdoin National Wildlife Refuge, northcentral Montana.

throughout much of their range, but relatively few data for these species are available from the northern mixed-grass prairie (Wheelwright and Rising 1993, Lanyon 1994, Vickery 1996).

We present 11 years of data on the reproductive biology of six grassland bird species that breed in mixed-grass prairie of northcentral Montana: Sprague's Pipit; Savannah, Grasshopper, and Baird's sparrows; Chestnut-collared Longspur; and Western Meadowlark. Our objectives were to characterize: (1) songbird community structure, (2) nesting phenology, (3) fecundity, (4) brood parasitism rates and nest success, and (5) to describe how these characteristics varied across years.

METHODS

Study Area.—Our study was conducted during 1997–2007 at Bowdoin National Wildlife Refuge (NWR) in Phillips County, near the town of Malta in northcentral Montana (48° 24′ N, 107° 39′ W; ~750 m asl). The study area consisted of five permanent sites (26–59 ha) totaling 218 ha of flat to gently rolling native mixed-grass prairie (Fig. 1). Data for this analysis were collected at four sites beginning in 1997. One of these sites partially (3 ha) burned in a wildfire in 1994, and was then prescribed burned during spring 2004; a second site was prescribed burned in spring 2007 and was not monitored during 2004. A fifth site, which had been prescribed burned during spring 2000, was added in 2001. No other burning events have occurred on the study sites since refuge documentation began in 1936. Grazing by cattle was gradually phased out during 1973–1977.

The climate is continental and semiarid, characterized by strong winds and high evaporation rates. Mean long-term annual and seasonal (May–Jul) precipitation totals are 34 and 18 cm, respectively (National Climatic Data Center 2007). Mild drought conditions prevailed during the study period; mean annual and seasonal precipitation totals were 32 and 14 cm, respectively (National Climatic Data Center 2007). The plant community was dominated by western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), and clubmoss (*Selaginella densa*). Invasive plant species were isolated and sparse. Shrubs (*Sarcobatus vermiculatus*, *Artemisia cana*, *Ceratoides lanata*) were sparse, and trees absent, except sporadically outside the periphery of two study sites.

Photographic records at Sprague's Pipit nests (n = 5) documented Northern Harrier (*Circus cyaneus*), garter snake (*Thamnophis* spp.), Western Meadowlark, and deer mice (*Peromyscus* spp.) preying upon nestlings during this study (S. L. Jones, unpubl. data). Other potential nest predators have been observed on, or within, the immediate vicinity of our study sites, including:

American badger (*Taxidea taxus*), long-tailed weasel (*Mustela frenata*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), mice and voles (*Zapus*, *Reithrodontomys*, and *Microtus*), Richardson's ground squirrel (*Spermophilus richardsonii*), bullsnake (*Pituophis melanoleucus*), prairie rattlesnake (*Crotalus viridis*), gulls (*Larus* spp.), Short-eared Owl (*Asio flammeus*), Loggerhead Shrike (*Lanius ludovicianus*), and Black-billed Magpie (*Pica hudsonia*).

Nest Searching.—Sites were searched for nests 3–5 times per week from early May through late July in an attempt to locate all active nests each year. Search techniques (% successful) included behavioral observations (3%) (Martin and Geupel 1993), opportunistic foot flushes (36%), and rope dragging (61%) (Davis 2003, Dieni and Jones 2003). Nests were marked for relocation by placing a discrete strip of plastic flagging on the ground ~2.5 m on either side of the nest. Nests were monitored every 2–4 days until the nesting outcome was ascertained. Nesting stage at initial discovery was assigned by candling eggs (Lokemoen and Koford 1996) or estimating age of nestlings (Jongsomjit et al. 2007). Nesting outcomes were: (1) successfully fledged at least one young of the parental species, (2) depredated, (3) abandoned (eggs or nestlings left permanently unattended), or (4) unknown. Observations of fledglings within 3 days of expected fledging, the presence of feces and feather scales in the nest, fledglings near the nest, and adults uttering alarm calls nearby or feeding new fledglings within 50 m of the nest were treated as evidence of reproductive success. Predation was assumed when the nest, eggs or nestlings too young to fledge disappeared or were destroyed.

Statistical Analysis.—Number of nests located for each focal bird species was summarized only for the three sites which had not been disturbed by prescribed fire to quantify annual variation of nesting density. Site effects were ignored given the relatively close spatial proximity of the study sites.

The nest was the primary sample unit for the analysis of reproductive parameters and nest success. Clutch initiation dates (CID) were estimated by calculating the date of clutch initiation from egg or nestling age or from known dates of major events (e.g., hatching). Reproductive parameters are reported using standard measures of central tendency. Data variation was summarized using the coefficient of variation (CV = SD/mean; Zar 1999); annual variation for many parameters was summarized only for the dominant species with adequate sample sizes. Trend lines (across years) were fit using the method of least squares; strength of trends was characterized using simple beta (b) and correlation (Pearson r) coefficients.

We estimated nest daily survival rates (DSR) using the survival model in program MARK (White 2008) for the six focal bird species, and to examine how DSR varied temporally across years (1997–2007). Program MARK uses a generalized linear approach to modeling DSR and maximum likelihood estimation to derive model coefficients and sampling variances (Dinsmore et al. 2002, Rotella et al. 2004). Regression models were constructed using the logistic transformation (logit) as the link function and natural logs [ln(DSR/1-DSR)]. Bird species and year were treated as nominal-scale variables (6 and 11 levels, respectively) with each level introduced into the regression model as an artificial explanatory variable and 0 or 1 coding; second-order interactions between species and year were added with the appropriate cross-product terms. One candidate model set was evaluated within an information-theoretic framework (Burnham and Anderson 2002). Program MARK was used to calculate Akaike's Information Criterion corrected for small sample sizes (AIC_c), ranking the fit of each model in ascending order of AIC_c values. Estimates for each species and year were calculated using the model-averaging approach (Burnham and Anderson 2002) weighted according to that model's likelihood in the set (normalized Akaike weight). The intercept-only model (where the regression coefficient was set to zero) was included in a set with the covariate of interest (species or year), which served to reduce model-selection bias of the estimate (Burnham and Anderson 2002). A point estimate of nest success was calculated as DSR raised to the mean number of days of the nesting period (incubation and nestling stages combined) for each species (Rotella 2007).

RESULTS

Nine species of passerines were actively breeding on our study area. Nests (n = 1,494) of the six focal species accounted for 98% of all passerine nests found during 1997–2007. Only a small number of nests of Horned Lark (*Eremophila alpestris*; n = 5), Lark Bunting (*Calamos-*

TABLE 1. Annual variation in nesting totals for six songbird species, Bowdoin National Wildlife Refuge, Montana. Numbers of nests discovered in the three undisturbed sites were summarized across years (1997–2006). Total nests were summarized across all songbird species encountered. Values are adjusted per 40 ha. Linear trends in nest totals across years are summarized using Pearson (r) and beta (b) coefficients.

Statistic	Sprague's Pipit	Savannah Sparrow	Grasshopper Sparrow	Baird's Sparrow	Chestnut-collared Longspur	Western Meadowlark	Total nests
Mean	2.7	4.6	2.7	1.5	15.4	2.6	30.4
CV	0.49	0.30	0.33	1.05	0.31	0.46	0.25
Min	1.3	2.8	1.5	0	10.7	0.8	20.6
Max	5.3	7.4	4.1	4.8	22.4	4.1	41.2
n	94	164	97	52	547	92	1,075
r	0.16	−0.64	0.14	−0.76	−0.53	−0.61	−0.56
b	0.1	−0.3	0.0	−0.4	−0.8	−0.2	−1.3

piza melanocorys; n = 7), and Vesper Sparrow (*Pooecetes gramineus*; n = 18) were found. Chestnut-collared Longspurs were the dominant breeding species accounting for over 51% of all passerine nests discovered over all years, followed by Savannah Sparrow (17%), Sprague's Pipit (8.4%), Grasshopper Sparrow (8.1%), Western Meadowlark (7.8%), and Baird's Sparrow (6%). Mean rank in nest abundance across all years followed a similar order: Chestnut-collared Longspur (1.0, CV = 0.0), Savannah Sparrow (2.2, CV = 0.20), Western Meadowlark (3.9, CV = 0.27), Grasshopper Sparrow (4.1, CV = 0.19), Sprague's Pipit (4.2, CV = 0.33), and Baird's Sparrow (5.6, CV = 0.18).

Annual variation in total nests was summarized collectively for three unburned study sites (Table 1). Annual variation (CV) in nest density ranged from 1.05 for Baird's Sparrow to 0.30 for Savannah Sparrow among focal species. Variability in total songbird nest density was moderate (CV = 0.25) ranging from 41 nests/40 ha in 1997 to 21 nests/40 ha in 2001. A modest declining trend for total songbird nests/40 ha was evident (b = −1.3, r = −0.56) across all years. This trend was pronounced for Baird's Sparrow (r = −0.76), but also evident for Savannah Sparrow (r = −0.64), Western Meadowlarks (r = −0.61), and Chestnut-collared Longspurs (r = −0.53). Nests were primarily discovered during incubation (67%) with frequency of nests discovered generally decreasing thereafter. Relatively few nests were discovered during the nest-building phase (Fig. 2).

Reproductive Parameters.—The CID frequency distribution for Chestnut-collared Longspurs was multimodal across all years, exhibiting three peaks. Bimodal distributions were evident for

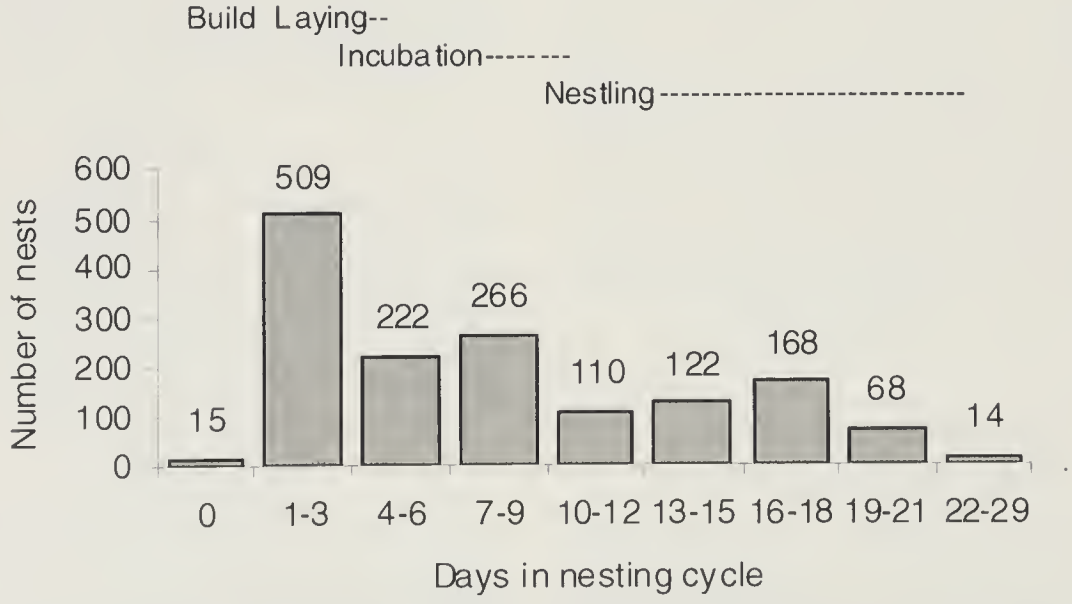

FIG. 2. Frequency distribution of nest age-intervals at time of discovery, Bowdoin National Wildlife Refuge, Montana, 1997–2007 (n = 1,494). Nests were primarily located during incubation with frequency of nests generally decreasing thereafter. Relatively few nests were located during the nest-building phase.

TABLE 2. Frequency distributions for clutch initiation dates (CID) for six songbird species at Bowdoin National Wildlife Refuge, Montana, 1997–2007. Values include peaks (modes), mean, and median nesting dates. Nesting period includes the range of activities observed across years for each species from the earliest CID date to last nest fledged. Frequency distributions were multimodal for three species and generally positively skewed towards early season breeding for all species.

Species	Nest peaks	Mean	Median	Earliest	Latest	Potential nesting period
Sprague's Pipit	23 May	5 Jun	25 May	7 May	31 Jul	07 May–25 Aug
Savannah Sparrow	24 May, 27 Jun	6 Jun	2 Jun	11 May	19 Jul	11 May–09 Aug
Grasshopper Sparrow	27 May	13 Jun	16 Jun	18 May	17 Jul	18 May–06 Aug
Baird's Sparrow	30 May	11 Jun	9 Jun	14 May	21 Jul	14 May–10 Aug
Chestnut-collared Longspur	21 May, 6 Jun, 15 Jun	7 Jun	7 Jun	30 Apr	19 Jul	30 Apr–10 Aug
Western Meadowlark	24 May, 2 Jun, 7 Jun	4 Jun	4 Jun	30 Apr	14 Jul	30 Apr–07 Aug

Savannah Sparrows and Western Meadowlarks; the remaining species were unimodal. All CID frequencies were positively skewed towards early-season breeding. On average, Sprague's Pipits were the earliest to nest (median date = 25 May) and Grasshopper Sparrows were the latest (median date = 16 Jun) (Table 2). All species ended clutch initiation by the end of July. The earliest fledging date observed was 26 May (Chestnut-collared Longspur) and the latest was 25 August (Sprague's Pipit). Variation in mean CID across years was low for Chestnut-collared Longspurs (SD = 2.9 days) and higher for Savannah Sparrows (SD = 5.6 days). The trend in CID across years was extremely weak for either species ($|b| \leq 0.20$ d, $|r| < 0.12$).

Variability (CV $\leq$ 0.18) in incubation and nestling phase duration was low, regardless of species (Table 3). Mean clutch size across all years ranged from 4.1 eggs (Chestnut-collared Longspurs) to 4.6 eggs (Sprague's Pipits). Mean clutch size did not vary considerably across years for either Chestnut-collared Longspurs (CV = 0.04) or Savannah Sparrows (CV = 0.06). Clutch size tended to decrease over the course of a season, regardless of bird species, although Sprague's Pipits and, to a lesser extent, Chestnut-collared Longspurs had increased clutch sizes during the first month of the breeding season (Fig. 3). Hatching rate (% of total eggs laid that hatched) across all years ranged from 88% for Chestnut-collared Longspurs and Grasshopper Sparrows to 78% for Savannah Sparrows. Hatching rates were similar for Sprague's Pipits (85%), Baird's Sparrows (84%), and Western Meadowlarks (82%).

Mean number of nestlings across all years ranged between 3.5 for Savannah Sparrows to 4.0

TABLE 3. Nest stage duration and reproductive parameters, by songbird species at Bowdoin National Wildlife Refuge, Montana, 1997–2007. Values represent mean ± CV (*n*; range). Fledged/nest represents the number of young fledged across all nests, regardless of nesting outcome.

Species	Nest stage (days)		Reproductive parameters			
	Incubation	Nestling	Clutch size	No. of nestlings	No. fledged/ successful nest	Fledged/nest
Sprague's Pipit	12.2 ± 0.12 (85; 7–15)	12.9 ± 0.18 (19; 9–17)	4.6 ± 0.17 (129; 1–6)	4.0 ± 0.26 (97; 1–6)	3.4 ± 0.35 (49; 1–6)	1.30 ± 1.07
Savannah Sparrow	11.6 ± 0.11 (184; 8–15)	10.1 ± 0.16 (73; 7–14)	4.3 ± 0.23 (260; 1–6)	3.5 ± 0.37 (191; 1–6)	3.2 ± 0.41 (101; 1–6)	1.23 ± 0.94
Grasshopper Sparrow	10.9 ± 0.14 (86; 7–13)	9.7 ± 0.17 (26; 7–12)	4.3 ± 0.24 (123; 0[a]–6)	3.9 ± 0.28 (95; 1–6)	3.6 ± 0.33 (64; 1–5)	1.89 ± 1.56
Baird's Sparrow	11.0 ± 0.10 (62; 7–14)	9.6 ± 0.11 (27; 8–11)	4.3 ± 0.19 (90; 2–6)	3.7 ± 0.31 (70; 1–5)	3.4 ± 0.36 (40; 1–5)	1.52 ± 1.31
Chestnut-collared Longspur	10.9 ± 0.12 (567; 7–15)	11.1 ± 0.16 (185; 7–15)	4.1 ± 0.20 (770; 1–7)	3.6 ± 0.27 (627; 0[a]–6)	3.4 ± 0.32 (342; 0[a]–5)	1.50 ± 1.37
Western Meadowlark	12.9 ± 0.12 (78; 8–15)	12.7 ± 0.10 (31; 9–16)	4.4 ± 0.30 (119; 0[a]–7)	3.8 ± 0.40 (89; 1–6)	3.2 ± 0.47 (46; 1–5)	1.24 ± 0.82

[a] Brown-headed Cowbird (*Molothrus ater*) only.

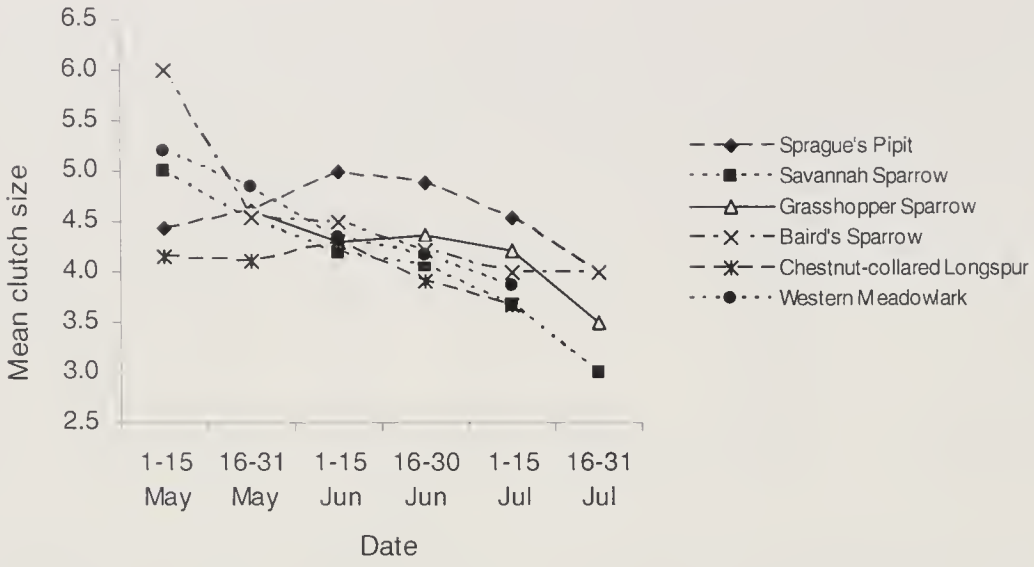

FIG. 3. Mean clutch size plotted against date by species across all years (1997–2007), Bowdoin National Wildlife Refuge, Montana. Mean clutch size generally decreased for each species as the nesting season progressed.

for Sprague's Pipits (Table 3). Grasshopper Sparrows had the highest fledging rate (1.9) across all nests in all years while Savannah Sparrows and Western Meadowlarks had the lowest (1.2) (Table 3). Variation in mean fledglings/nest across years was low for Chestnut-collared Longspurs (CV = 0.20) with a modest decreasing trend across years ($b = -0.05$, $r = -0.59$). This statistic was more variable for Savannah Sparrows (CV = 0.45), but with no discernable trend ($r = -0.09$).

Nest Success.—DSR across all species and years was estimated at 0.947 (SE = 0.002). There was little statistical support for species-specific variation in DSR (Table 4). Model-averaged estimates for each species (Table 5) indicated little variation in DSR among species. However, variation in DSR across years was evident, suggesting a decline during the study period ($b = -0.002$, $r = -0.54$) (Fig. 4). There was little statistical support for an interaction between species and year (Table 4).

Nest depredation accounted for 82% of all known nest failures with most (71%) during the nestling stage. Desertion (abandonment) was judged to be the cause for 18% of all known nest failures. Cause of abandonment was discernable in only 27% of these cases; 25% ($n = 38$) were attributed to severe weather (e.g., heavy rain, hailstorms), 1% ($n = 2$) to observer activities, and 1% ($n = 2$) to Brown-headed Cowbird brood parasitism. Brown-headed Cowbird parasitism rates ranged from 2% for Chestnut-collared Longspurs to 26% for Western Meadowlarks (Table 6).

TABLE 4. Model set exploring the relationship between bird species (6 levels) and year (1997–2007) at Bowdoin National Wildlife Refuge, Montana on nest daily survival rate (DSR) using Akaike's Information Criterion, corrected for small sample sizes (AIC_c). Delta AIC_c (AIC_c model i – AIC_c minimum), Akaike weight (w_i), and number of parameters (K) are included for each model.

Model	Δ AIC_c	w_i	K
Year	0.0	0.66	11
Species + year	1.5	0.31	16
Intercept	6.8	0.02	1
Species	10.7	0.00	6
Species*year	10.7	0.00	63

DISCUSSION

Songbird community structure based on nesting density was relatively stable across the 11-year period of this study. Chestnut-collared Longspurs were clearly the dominant nesting species every year. Savannah Sparrows were the second most abundant bird species during all but 2 years, while Baird's Sparrows were least abundant among focal species during all but 2 years. Few to no nests of shortgrass prairie obligates, such as Horned Lark or McCown's Longspur (*Calcarius mccownii*) were located. Chestnut-collared Longspurs generally breed in drier, shortgrass to short–mixed-grass prairie, while Sprague's Pipits and Baird's Sparrows range across the breadth of mixed-grass prairie grassland types (Knopf 1996). Our assemblage of breeding songbirds, in addition to plant community composition and structure (Dieni and Jones 2003), classify our study area as

TABLE 5. Estimated nest DSR for six bird species across all years at Bowdoin National Wildlife Refuge, Montana, 1997–2007. Standard errors (SE), lower (LCI) and upper (UCI) 95% confidence limits, and number of nests (n) are included. Nest success equals DSR raised to the mean number of days of the nesting period (incubation and nestling stages combined) for each species.

Species	DSR	SE	LCI	UCI	n	Nesting period	Nest success
Sprague's Pipit	0.947	0.003	0.942	0.952	128	25.1	0.27
Savannah Sparrow	0.946	0.004	0.938	0.953	255	21.7	0.25
Grasshopper Sparrow	0.948	0.004	0.940	0.955	121	20.6	0.39
Baird's Sparrow	0.947	0.003	0.940	0.953	90	20.6	0.32
Chestnut-collared Longspur	0.947	0.002	0.943	0.951	759	22.0	0.31
Western Meadowlark	0.947	0.003	0.941	0.952	118	25.6	0.25
Totals	0.947	0.002	0.943	0.950	1,471	22.3	0.30

xeric short–mixed-grass prairie (Knopf 1996, Askins et al. 2007).

Breeding Bird Survey data indicate long-term (1966–2007) declines in rangewide populations for all our focal bird species (Sauer et al. 2008). In particular, rangewide populations of two mixed-grass endemics, Sprague's Pipit (-3.9, $P = 0.00$, $n = 169$) and Baird's Sparrow (-3.4, $P = 0.01$, $n = 141$), as well as Chestnut-collared Longspur (-2.8, $P = 0.00$, $n = 160$) have exhibited steep declines (Sauer et al. 2008). We recorded general declines in nest density for most of our study species on undisturbed study sites, although no discernable trend was observed for Sprague's Pipit or Grasshopper Sparrow. The decline in nesting density of Baird's Sparrow may be a function of drier than normal climatic conditions that prevailed over most of the study period (National Climatic Data Center 2007). Our study area possessed none of the habitat conditions that are commonly the result when the northern mixed-grass prairie is left idle (Madden et al. 1999). The prevalence of invasive plant species and woody-vegetation encroachment remained low, while forbs were abundant during the course of the study (S. L. Jones, unpubl. data). Moreover, xeric mixed-grass prairie historically had lengthy periods without grazing, and natural burn frequencies that often ranged between 8 and 26 years (Askins et al. 2007).

We used nest density as an index to bird abundance to gauge community structure and trend, but nest density clearly does not equate directly to bird or even territorial density. Some species we studied have been documented to have multiple broods in a season. Our population was marked for only a few species and years (Jones et al. 2007); it was not possible in most cases to distinguish single broods by different individuals from multiple broods after a successful nest or re-

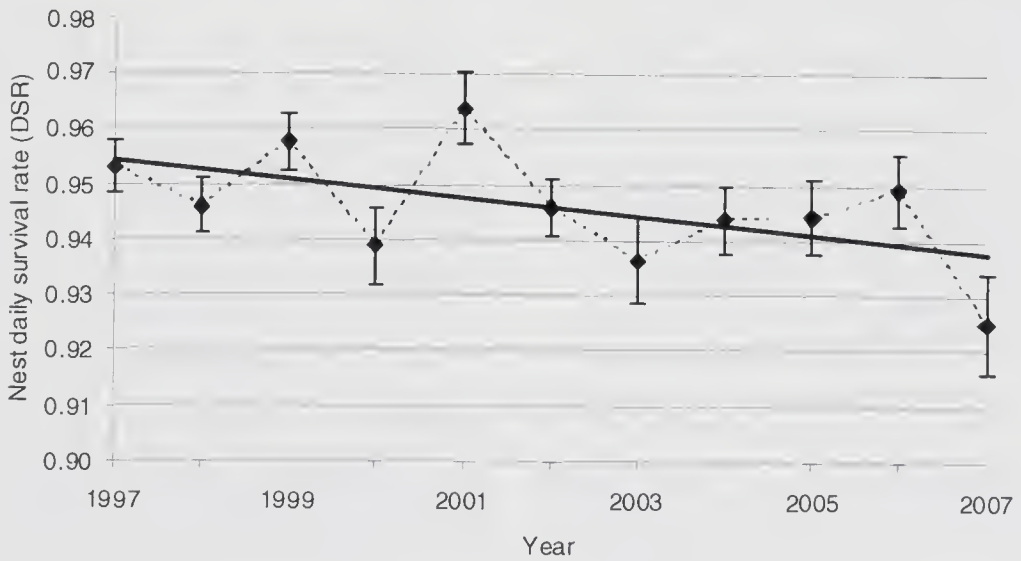

FIG. 4. Annual variation in daily survival rates of songbird nests (DSR ± SE) at Bowdoin National Wildlife Refuge, Montana. There was considerable annual variation in DSR (annual mean = 0.946 ± 0.011 CV). A declining trend in DSR was evident ($b = -0.002$, $r = -0.54$).

TABLE 6. Nesting outcome and parasitism rates for each bird species across all years, 1997–2007 at Bowdoin National Wildlife Refuge, Montana. Most monitored nesting attempts were unsuccessful with the majority of failures attributed to nest predation. Weather events (e.g., hail) were collectively the leading known cause of nest desertion. Parasitism by Brown-headed Cowbirds resulted in only a few nest failures.

						Brown-headed Cowbird parasitism		Known causes of abandonment (*n*)		
Species	Successful	Depredated	Abandoned	Unknown	*n*	Relative frequency	Total cowbirds fledged	Weather	Observer disturbance	Parasitism
Sprague's Pipit	0.37	0.57	0.06	0.00	128	0.02	2	1	0	0
Savannah Sparrow	0.40	0.43	0.17	0.01	260	0.13	17	15	1	1
Grasshopper Sparrow	0.52	0.35	0.12	0.01	123	0.04	2	3	0	0
Baird's Sparrow	0.43	0.42	0.16	0.00	89	0.04	0	4	0	0
Chestnut-collared Longspur	0.44	0.48	0.07	0.01	770	0.02	3	11	0	1
Western Meadowlark	0.40	0.45	0.14	0.00	119	0.26	18	4	1	0
n	637	688	151	13	1,489	91	42	38	2	2

nesting after nest failure. However, Savannah Sparrows, Chestnut-collared Longspurs, and Western Meadowlarks all had multimodal CID distributions suggesting at least some community members may have had several clutches per year. None of the species we studied has been documented with more than two successful broods per year (Wheelwright and Rising 1993, Lanyon 1994, Vickery 1996, Hill and Gould 1997). Sprague's Pipit, and Baird's and Grasshopper sparrows had only single frequency peaks in our CID data, which suggests a tendency towards a single brood per season. This contrasted with Vickery (1996), who reported Grasshopper Sparrows in general have a protracted breeding season, often producing ≥2 broods annually, even in the northern portion of their range. Sprague's Pipit and Baird's Sparrow have only rarely been documented to have multiple broods in a season (Robbins and Dale 1999, Green et al. 2002). Second broods after successfully fledging young have been documented twice for Sprague's Pipit (Sutter 1996, Davis 2009). Re-nesting after nest failure has been rarely documented for this species (Sutter 1996, Davis 2009), as has polygyny (n = 1) (Dohms and Davis 2009). Baird's Sparrow in southwest Manitoba (Davis and Sealy 1998) and in our study had a second, smaller nest initiation peak in mid to late June, suggesting second broods or re-nesting attempts; second broods have only been documented twice (Davis and Sealy 1998; S. L. Jones, unpubl. data).

Mean CID for Savannah Sparrows and Chestnut-collared Longspurs varied little across years. Mean clutch size also had little variation among seasons; however, a within-season declining pattern was evident for this parameter for all species. Similar patterns have been documented elsewhere for these bird species (Vickery 1996, Davis and Sealy 1998, Winter 1999, Davis 2003). Sprague's Pipits were a notable exception in our study, where clutch size generally increased during the first month of the breeding season. A similar pattern was also reported for Sprague's Pipit in Saskatchewan (Davis 2003). Clutch size in our study linearly decreased over the course of the breeding season for Western Meadowlarks, which contrasted with a study in Manitoba, where Western Meadowlarks had peak clutch size during mid-season (Lanyon 1994).

Brown-headed Cowbird parasitism rates, except for Western Meadowlark, were relatively low in our study (2–13%). Much higher rates were reported for our focal species in southwest Manitoba: Sprague's Pipit = 18%, Savannah Sparrow = 32%, Grasshopper Sparrow = 29%, Baird's Sparrow = 37%, and Chestnut-collared Longspur = 14% (Davis and Sealy 2000). Our rate for Western Meadowlark (26%) was low compared to rates reported in Manitoba (43%) (Davis and Sealy 2000), and North Dakota (47%) (Koford et al. 2000), but were consistent with reported rates in Saskatchewan (25%) (Davis 2003). Chestnut-collared Longspurs and Sprague's Pipits had the lowest parasitism rates in our study, which is consistent with findings in other studies (Hill and Gould 1997, Davis and Sealy 2000, Davis 2003). Several factors may be

responsible for the relatively low levels of parasitism found in our study area (i.e., large patches of continuous grassland, a landscape with few potential perches, relatively little shrub and tree cover, and no cattle grazing). All of these factors directly enhance Brown-headed Cowbird parasitism rates (Davis and Sealy 2000, Koford et al. 2000).

Nest depredation is commonly the single most important factor affecting nesting success in cup-nesting passerines (Ricklefs 1969); depredation rates have been generally high throughout the mixed-grass prairie (Vickery et al. 1992; Winter 1999; Davis 2003, 2005; Winter et al. 2005). Nest predation accounted for the majority of observed nest failures in our study, mainly during the nestling stage. This is a common pattern among passerines; greater parental activity at the nest, as well as greater olfactory cues, noise, and movements by nestlings are thought to increase the likelihood of nest detection by predators (Halupka 1998).

Overall nest success for Sprague's Pipits was estimated to be much higher in southwest Manitoba (47%, Davis and Sealy 1998) than estimated in our study area (27%). Grasshopper Sparrow and Western Meadowlark nesting success rates were comparable to those reported by Lanyon (1994) and Vickery (1996). Our estimate of nest success (32%) for Baird's Sparrow was higher than reported in Saskatchewan (26%, Davis 2003), but lower than in Manitoba (54%, Davis and Sealy 1998). Nest success for Chestnut-collared Longspurs was higher in Alberta (56%, Hill and Gould 1997) than estimated for our study area (44%; Table 6).

DSR estimates did not differ markedly among bird species, suggesting that factors such as weather and the predator community were affecting all bird species equally. Therefore, those elements affecting nest success that vary with year (i.e., predator community or weather) probably influenced the members of this grassland songbird community in a similar manner in a given year.

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MOUNTAIN BIKING TRAIL USE AFFECTS REPRODUCTIVE SUCCESS OF NESTING GOLDEN-CHEEKED WARBLERS

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ABSTRACT.—We evaluated foraging and nesting behavior, territory size, and nest success of Golden-cheeked Warblers (*Dendroica chrysoparia*), a federally endangered songbird, relative to mountain biking trail use. We conducted our study at two mountain biking sites and two control sites at Fort Hood Military Base and in Austin, Texas, in spring 2002 and 2003. Territories of male Golden-cheeked Warblers in biking sites (2.2 ha) were >1.5 times as large as those in non-biking sites (1.4 ha). Mayfield nest success in biking sites (n = 33) was 35% compared to 70% in non-biking sites (n = 22). Nest abandonment was three times greater in biking areas (15%) than non-biking areas (5%). Seven nests were depredated in biking sites, but only two nests were depredated in non-biking sites. Texas rat snakes (*Elaphe obsoleta*) were the most frequent nest predator at biking sites, accounting for 71% of the predations. We conducted behavioral observations of male Golden-cheeked Warblers in biking (n = 139) and non-biking (n = 204) sites. Males spent similar amounts of time in diurnal behaviors in biking and non-biking sites. We used video-camera systems to record female nesting behaviors at 17 nests in biking sites and 15 nests in non-biking sites. Nesting behaviors of females did not differ between biking and non-biking sites. The cumulative effect of disturbance from mountain biking trail use on Golden-cheeked Warbler foraging and nesting behavior appears to be minimal, but fragmentation and alteration of habitat by mountain biking trails may reduce quality of nesting habitat for Golden-cheeked Warblers. *Received 23 November 2009. Accepted 27 March 2010.*

Mountain biking is one of the fastest-growing outdoor recreational activities in the United States, experiencing substantial growth in the last 20 years (Mosedale 2002, Pike Masteralexis et al. 2008). This increase has led to greater demands for quality outdoor experiences on trail networks in areas that often contain fragile environments (Flather and Cordell 1995). Land managers have raised concerns about the impacts of mountain biking activities on natural resources (Chavez et al. 1993, Symmonds et al. 2000). These concerns led to restrictions in mountain biking activities at all federal wilderness areas and many other public lands in the United States despite little scientific insight on their impacts to wildlife (Taylor and Knight 2003).

The Golden-cheeked Warbler (*Dendroica chrysoparia*) is a federally endangered species that breeds exclusively in the mature juniper (*Juniperus ashei*)-oak (*Quercus* spp.) woodlands of central Texas (Ladd and Gass 1999). Some of its breeding range is used by mountain bikers (e.g., Dinosaur Valley State Park in Somervell County, Lost Maples State Natural Area in Bandera County, Belton Lake Outdoor Recreation Area [BLORA] in Bell County, and Emma Long Metropolitan Park [ELMP] in Travis County). Increased levels of predation on passerine nests near mountain biking trails have been documented (Miller et al. 1998, Miller and Hobbs 2000). Mountain biking also may alter distribution and behaviors of Golden-cheeked Warblers. In particular, disturbance from mountain biking may lessen the time and energy used for fitness-enhancing activities including feeding, nest attentiveness, mate attraction, and territory defense (Knight and Gutzwiller 1995).

Disturbance from mountain biking activities may pose a threat to successful breeding of Golden-cheeked Warblers; a Biological Opinion issued by the U.S. Fish and Wildlife Service (USDI 1993) and a regional "take" permit issued by the U.S. Fish and Wildlife Service under the umbrella of the Balcones Canyonlands Conservation Plan recommended eliminating and restricting mountain biking activities from Golden-cheeked Warbler habitat in areas of the Fort Hood Military Reservation and Travis County, respectively. Those recommendations were controversial, and further research of the impacts of mountain biking on Golden-cheeked Warblers was needed. Our objectives were to examine effects of mountain biking trail use on foraging

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and nesting behavior, territory size, and nest success of Golden-cheeked Warblers.

METHODS

Study Area.—We conducted this study at two mountain biking sites and two control sites from March to June, 2002 and 2003. The mountain biking sites were at BLORA in Fort Hood Military Reservation (31° 06′ N, 97° 31′ W) and ELMP (30° 19′ N, 97° 50′ W) in Balcones Canyonlands Preserve (BCP) in Austin, Texas. Control sites were at Training Area 13A (13A) on Fort Hood Military Base (30° 10′ N, 97° 45′ W) and Forest Ridge Preserve (FRP; 30° 24′ N, 97° 55′ W) in BCP. Recreational activities were restricted from both control areas, and military activities were restricted on both sites at Fort Hood. Mountain biking activities, as measured by TrailMaster photoelectric trail counters placed along trails, averaged 15 mountain bikers/day (5 bikers/day at BLORA and 17 bikers/day at ELMP) and ranged from zero to 30 bikers/day at biking sites (Davis and Leslie 2008). Mountain bikers accounted for >80% of the trail users at biking sites. Other users recorded at biking sites included motorized bikers (<2%), hikers and joggers (2%), and researchers (11%).

Fort Hood and BCP are within the Crosstimbers and Southern Tallgrass Prairie and Edwards Plateau ecoregions, respectively. Fort Hood contains ~21,850 ha of Golden-cheeked Warbler habitat and supports the largest known population of Golden-cheeked Warblers under one management authority (USDI 1993); the BCP contains ~10,600 ha of preserve properties with 5,300 ha of Golden-cheeked Warbler habitat (Reidy et al. 2008). Mountain biking sites ranged in size from 116 (ELMP) to 192 ha (BLORA), and control sites ranged in size from 190 (FRP) to 198 ha (13A). All sites were woodlands associated with steep limestone canyons and plateaus dominated by Ashe juniper and a variety of oaks.

Territory Size.—We used spot-mapping (Ralph et al. 1993) to delineate territories for color-banded and unbanded males at each site from 10 March to 24 June 2002 and 2003. Males were color banded from previous studies (at the BLORA site) and during our study. We used conspecific playback to capture males with 6-m mist nets. We banded males with unique color combinations of two or three plastic color bands and a numbered aluminum U.S. Geological Survey band. Individual locations of males were identified by standing directly under the location where a male was observed and using a handheld global positioning system unit (GPS; Garmin GPS III+, Garmin International, Olathe, KS, USA) to record Universal Transverse Mercator (UTM) coordinates. We recorded one location of each individual during a single visit, but attempted to obtain locations at different time periods throughout the day. We later plotted locations of individuals on 1:4,000 digital orthoquad maps with 1.5-m resolution imagery and a 500 × 500-m grid overlay to distinguish territories throughout each year. We distinguished individual territories by identifying color bands. We relied on countersinging by unbanded males that occupied adjacent territories as well as a general familiarity of an individual's territory as the season progressed to facilitate delineation of territories. We attempted to obtain ≥30 locations per individual male (Laundre and Keller 1984, Bibby and Burgess 1992, Seaman et al. 1999). We used the Home Range extension in ArcView and 1,000 iterations of the bootstrap procedure to calculate the minimum number of male locations sufficient for a reliable minimum convex polygon (MCP) estimate (Rodgers and Carr 1998, ESRI 2000). We calculated that 33 locations were sufficient for estimating the MCP for males on the basis of the bootstrap procedure. We estimated MCP using the Home Range extension in ArcView for those males with a minimum of 33 locations.

We characterized land cover types within each study site and each territory using the National Land Cover Database (NLCD) of 2001 to evaluate whether territories differed by habitat composition. Land-cover categories in the NLCD were reclassified into eight broad categories (water, bare ground, deciduous forest, evergreen forest, mixed forest, shrub/scrub, grassland, and wetland) to standardize our analysis across the four study sites. The proportions of landcover types from NLCD (i.e., forested, grassland) within each bird's home range were extracted in ArcView. We walked all trails within each study area using a GPS unit (Trimble Geoexplorer 3, Trimble Navigation Ltd., Sunnyvale, CA, USA) to delineate trails. We downloaded trail locations and created a Geographic Information System (GIS) cover layer of trails for each study site using ArcView.

Time Activity Budgets of Territorial Males.—We assessed the impact of mountain biking activity on foraging activities by conducting

behavioral observations of males on territories at each study site from March to June, 2002 and 2003. We conducted observations throughout the day. We minimized sampling bias due to diurnal variation in foraging behavior by collecting behavioral data equally during three time periods: early, sunrise to 1100 hrs; mid-day, 1101 to 1500 hrs; and late, 1501 hrs to sunset. Males were located by listening for a Type A- or B-song. We predominantly observed males using binoculars, but, in some cases, observed males directly. We attempted to observe each bird for 300 sec and discarded observation sessions <30 sec in length. We dictated behaviors into a handheld microcassette tape-recorder. We avoided bias toward conspicuous behaviors by not recording behaviors until 5 sec after locating a bird (Wunderle and Latta 1998). We used focal individual sampling (Altmann 1974, Martin and Bateson 1986) to collect behavioral data. We avoided autocorrelation for banded birds by not recording behavior from the same individual more than once in a single day. We did not collect behavioral observations during inclement weather (rain or high wind).

We classified behaviors into nine categories (Robinson and Holmes 1982, Remsen and Robinson 1990): singing, preening, agonistic, mate guarding, perching (resting), locomotion (flying and hopping), foraging (searching, attacking, and food handling), feeding fledgling, and time-out (time when the bird was out-of-sight). The bird was considered in "time-out" when a focal male briefly disappeared behind vegetation during an observation. The tape recorder continued to run during the "time-out" period, and observations resumed when the bird reappeared. We ended the observation at the end of the last observation before the "time-out" if the bird did not reappear within the 300-sec period.

We further examined foraging activities in 2003 by recording the amount of time a male was engaged in searching, attacking, and food-handling. Search behaviors were considered to be any movements leading up to locating and acquiring food, and included hops (leg powered movements <10 cm), short flights (<20 cm), medium flights (20 cm to 2 m), and long flights (>2 m). Attack maneuvers were any movements directed at a food item or the substrate that concealed the food item after it was located and included gleaning, reaching, hanging, leaping, sally-striking, sally-hovering, and flutter-chasing (Remson and Robinson 1990).

Parental Behavior at Nests.—We assessed the impact of mountain biking trail use on nesting and parenting activities of Golden-cheeked Warblers by video-recording nests using miniature video camera systems (Fuhrman Diversified Inc., Seabrook, TX, USA). We relied on video-recordings in 2002 provided by another researcher studying nest predation of Golden-cheeked Warblers at Fort Hood sites (M. M. Stake, University of Missouri, Columbia, USA); we collected nesting and parenting behavior in 2003 using eight miniature video camera systems at the Fort Hood and Austin sites. Protocols for video-recording were similar for 2002 and 2003. Each system consisted of a 32- by 32- by 60-mm camera with a small lens and six infra-red diodes (950 nm) that allowed filming at night, an articulating arm that supported the camera, and a clamp at the base of the arm for attachment to a substrate. A video recorder, allowing 24 hrs of footage (~7 frames/sec) on a 120-min VHS cassette tape, was connected to the camera with a 20-m cable and powered by a 12-V rechargeable battery. We used a hand-held monitor connected to the cable for positioning the lens at the nest during set-up and connected to the base set-up to check nest status each day without approaching the nest. We changed tapes daily and replaced batteries every other day.

We generally found nests opportunistically during location of focal males. Most nests were found by following an adult to the nest during building and nestling stages. We set up cameras at nests, if accessible, and if cameras were available; nests found in the egg stage were prioritized for cameras but nests in the nestling stage were used as cameras became available. Cameras were typically installed in the afternoon to reduce risk of Brown-headed Cowbird (*Molothrus ater*) parasitism. We only installed cameras after the laying stage to reduce the risk of female abandonment (Stake 2000, Stake and Cimprich 2003, Stake et al. 2004, Reidy et al. 2008) and removed cameras if females did not resume activity at the nest within 1 hr. We were only able to monitor female activity at nests during incubation and nestling stages. Nests were monitored daily by video until nest fate was known (e.g., fledged young, depredated, abandoned, failed due to weather).

We watched tapes using a multispeed video player. Tapes for individual nests were viewed until the nest was no longer active. We recorded behaviors during the incubation stage, early

nestling stage, and late nestling stage. Behaviors recorded included female incubating eggs, female brooding nestlings, female or male provisioning nestlings, female shading nestlings, female or male perching and scanning at the nest, and male feeding the female. Females brood recently hatched nestlings for long periods during the first 3 days after hatching and continue brooding for 1–2 days thereafter (Ladd and Gass 1999); thus, we designated the early nestling stage as the first 5 days of the nestling stage. We recorded a variety of behaviors, but focused on incubation, brooding nestlings, and provisioning nestlings because changes in these behaviors may affect nest success (Gill 2007). Specifically, we focused on percent time spent incubating, number of incubation bouts/day and length of incubation bouts during the incubation period, and percent time spent brooding and provisioning nestlings, number of brooding and provisioning bouts/day, and length of brooding and feeding bouts during the early and late nestling stage.

Nest Success.—We assessed effects of mountain bike trail use on Golden-cheeked Warbler nesting success by monitoring all nests located at the study sites. Most of the nests (90%) were monitored with video; we monitored nests without cameras every 2–5 days until near fledging at which time we visited daily to more accurately monitor nests and correctly identify nest outcome. We considered a nest to be successful if ≥1 host young fledged. We considered a nest depredated if a predator removed at least one egg or nestling while the nest was active, and a nest abandoned if the male and female were absent from the nest after several days and the eggs or young were still present. We were able to identify all predation events to species-level from watching tapes. Successful production of ≥1 fledgling was confirmed by locating fledglings being fed by a parent (usually verified the day of or day after fledging), or by recording fledging by video surveillance.

Statistical Analyses.—We calculated area of trails by multiplying the linear length of trails within each MCP by 2.5 m, considered the average width of trails (AEG, pers. obs.). We used one-way analysis of variance (ANOVA) to examine differences in territory size, amount of trail area within each MCP, and habitat composition (% developed, % deciduous, % juniper, and % grassland) between biking and non-biking areas.

Some banded males had multiple foraging observations within time periods, and we averaged behaviors for those individuals within each time period prior to conducting analyses. We analyzed time-activity data using multivariate analysis of variance (MANOVA) with a factorial arrangement (SYSTAT 2004). Treatment (biking and non-biking), time period (early, mid-day, and late), and year (2002 and 2003) were independent factors in the MANOVA. We used MANOVA because the dependent variables (i.e., individual behaviors) were not independent of each other (i.e., the amount of time engaged in one behavior influenced the amount of time engaged in other behaviors). Wilks' lambda (λ) was the test criterion.

We used univariate analysis of variance (ANOVA) to examine differences in individual behaviors between years if the overall MANOVA was significant (Barker and Barker 1984). Behavioral data met assumptions of normality and homogeneity (Johnson and Wichern 1988, SYSTAT 2004). We used a similar MANOVA with factorial arrangement to analyze foraging search behavior data. We used Kruskal-Wallis tests, because of our small sample size, to compare food capture techniques (i.e., proportion of attack modes used by each male during foraging) of males between biking and non-biking sites.

There was considerable variability in amount of time each nest was videotaped (which could overemphasize the activities at some nests); thus, we calculated parental behavior parameters on a daily basis. We compared parental behavior parameters using Kruskal-Wallis tests.

We used Mayfield's (1961, 1975) method to calculate daily nest survival rates (DNS) for incubation and nestling stages, and nest success for biking (incubation: 111 nest-days, nestling: 146 nest-days) and non-biking (incubation: 69 nest-days, nestling: 108 nest-days) sites. We calculated standard errors for DNS following Johnson (1979). All statistical tests were considered significant at $P \leq 0.05$.

RESULTS

Territory Size.—Territory size for male Golden-cheeked Warblers averaged 1.5 times larger in biking than non-biking sites (Table 1). Territories ranged from 0.48 to 7.27 ha in biking sites and 0.24 to 4.33 ha in non-biking sites. Trails occupied twice the area within territories of Golden-cheeked Warbler males in biking than

TABLE 1. Mean ± SE for minimum convex polygon (MCP) territory size (ha), trail area (ha) within MCPs, and habitat composition (%) within MCPs for Golden-cheeked Warblers at biking and non-biking sites near Austin and on Fort Hood, Texas, during spring 2002–2003.

Variable	Biking (n = 30)	Non-biking (n = 61)	F^a	P
Territory size (MCP)	2.16 ± 0.19	1.43 ± 0.16	6.01	0.016
Trail area within MCP	0.068 ± 0.009	0.029 ± 0.004	9.77	0.002
Habitat composition				
Developed	0.67 ± 0.42	0.00 ± 0.00	1.21	0.274
Deciduous	6.00 ± 1.50	3.48 ± 2.70	0.78	0.378
Juniper	92.00 ± 1.78	96.52 ± 2.70	2.05	0.155
Grassland	1.34 ± 0.83	0.00 ± 0.00	1.27	0.262

[a] F and P values for analysis of variance comparisons between biking and non-biking sites; df = 1,89.

non-biking sites (Table 1). Habitat composition of territories did not differ between sites (Table 1).

Time Activity Budgets of Territorial Males.—We made 400 total observations (1–7 observations/male, 100–120 unique males) of male Golden-cheeked Warblers during the 2 years of study. Overall behavior did not differ between biking and non-biking sites (Wilks' $\lambda = 0.97$, $P = 0.265$; Table 2) and time periods (Wilks' $\lambda = 0.95$, $P = 0.365$), but differed between years (Wilks' $\lambda = 0.87$, $P < 0.001$). There were no significant two- or three-way interactions (Wilks' $\lambda \geq 0.93$, $P \geq 0.116$). Singing and provisioning nestlings were the only behaviors that differed between years. Male Golden-cheeked Warblers spent less time singing in 2002 than 2003 (8.3 vs. 16.0%) and more time provisioning nestlings in 2002 than 2003 (1.2 vs. 0.1%).

Prey search behaviors of male Golden-cheeked Warblers did not differ between biking and non-biking sites (Wilks' $\lambda = 0.97$, $P = 0.677$; Table 3). The total number of search bouts during each observation period also did not differ between biking and non-biking sites ($F_{1,93} = 0.03$; $P = 0.866$; $\bar{x} \pm$ SE = 26.2 ± 4.4 bouts vs. 27.2 ± 3.2 bouts). Male Golden-cheeked Warblers spent similar amounts of time engaged in attack techniques to capture prey at biking and non-biking areas (Table 4).

Parental Behavior at Nests.—We video-recorded 32 Golden-cheeked Warbler nests (17 in biking sites vs. 15 in non-biking sites) for 4,094.5 daytime hrs in 2002 and 2003 (incubation stage: 1,141.2 hrs for nests at biking sites and 828.2 hrs for nests at non-biking sites; nestling stage: 1,109.7 hrs for nests at biking sites vs. 1,015.4 hrs for nests at non-biking sites). Average recording time per nest was 110.6 ± 17.4 hrs (range = 15.2–432.8 hrs). Golden-cheeked Warblers spent similar amounts of time incubating eggs, brooding nestlings, and provisioning nestlings in biking and non-biking sites (Table 5). The number of bouts and length of the bout for each of these behaviors also did not differ between biking and non-biking sites (Table 5).

TABLE 2. Diurnal time activity budget ($\bar{x}$ ± SE) for male Golden-cheeked Warblers at biking (n = 139) and non-biking (n = 204) locations near Austin and on Fort Hood, Texas during spring 2002–2003.

	Day time (%)			
	2002		2003	
Behavior	Biking	Non-biking	Biking	Non-biking
Perching	37.5 ± 4.9	26.8 ± 3.5	29.9 ± 2.6	31.4 ± 2.2
Singing	7.8 ± 0.9	8.7 ± 0.9	15.6 ± 1.3	16.3 ± 1.2
Preening	10.2 ± 3.3	7.6 ± 2.4	5.9 ± 1.3	6.7 ± 1.3
Agonistic	0.0 ± 0.0	0.2 ± 0.1	0.6 ± 0.5	0.2 ± 0.1
Mate guarding	0.2 ± 0.2	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
Locomotion	38.8 ± 5.1	49.7 ± 4.2	44.6 ± 3.1	42.0 ± 2.5
Foraging	4.0 ± 1.0	3.9 ± 0.8	2.5 ± 0.5	3.0 ± 0.6
Food handling	0.9 ± 0.5	1.4 ± 0.7	0.6 ± 0.4	0.3 ± 0.2
Feeding fledgling	0.6 ± 0.3	1.7 ± 0.6	0.1 ± 0.1	0.1 ± 0.1

TABLE 3. Food searching behaviors ($\bar{x}$ ± SE) for male Golden-cheeked Warblers at biking (n = 41) and non-biking (n = 54) sites near Austin and on Fort Hood, Texas during spring 2003.

Behavior	Percent of total food searching time	
	Biking	Non-biking
Hop	59.4 ± 5.0	59.8 ± 4.0
Short flight, <20 cm	10.7 ± 1.9	11.6 ± 2.2
Medium flight, 20 cm–2 m	5.4 ± 1.2	7.4 ± 1.3
Long flight, >2 m	24.5 ± 5.0	21.1 ± 4.3

Nest Success.—We monitored 33 nests in biking sites and 22 nests in non-biking sites. Twenty-one (64%) and 19 nests (86%) successfully fledged at least one host young in biking and non-biking sites, respectively. Seven nests failed due to predation in biking sites, compared to two in non-biking sites. Texas rat snakes (*Elaphe obsoleta*) accounted for most of the depredation (71%) in biking sites, and American Crows (*Corvus branchyrynchos*) and fire ants (*Solenopsis invicta*) each accounted for one depredation in biking sites. Texas rat snakes and Cooper's Hawks (*Accipiter cooperii*) accounted for the two depredations in non-biking sites. Nest abandonment was three times higher in biking sites (5 nests; 15%) than non-biking sites (1 nest, 5%). The abandonments occurred either late in the laying stage or early in the incubation stage. We did not document parasitism by Brown-headed Cowbirds.

Daily nest survival for biking sites was 0.964 ± 0.018 for the incubation stage and 0.945 ± 0.019 for the nestling stage, whereas DNS for non-biking sites was 0.986 ± 0.014 for the incubation stage and 0.981 ± 0.013 for the nestling stage. The Mayfield nest success estimate in non-biking sites (70%) was twice as high as in biking sites (35%).

DISCUSSION

Our results suggest mountain biking trail use negatively impacted Golden-cheeked Warblers during the breeding season. Male territories were >1.5 times larger and nest success was substantially lower in biking than non-biking sites. Nest abandonment and predation were also higher in biking than non-biking sites. Several studies have suggested that habitat fragmentation negatively impacts Golden-cheeked Warbler nest survival (Fink 1996; Maas-Burleigh 1998; Peak 2007; Reidy et al. 2008, 2009). Peak (2007) reported nest survival of Golden-cheeked Warblers was lower in woodlands with high forest edge. Similarly, Reidy et al. (2009) reported that as edge factors including open edge density and amount of open edge increased, nest survival of Golden-cheeked Warblers substantially declined. Golden-cheeked Warbler territories in biking sites in our study occurred in habitats more fragmented by trails than territories in non-biking sites. It appears mountain biking indirectly affected Golden-cheeked Warblers by habitat alteration and fragmentation caused by occurrence of mountain biking trails.

Territory size in many bird species is inversely related to food abundance (Mahler 1970, Gass et al. 1976, Salmonson and Balda 1977, Smith and Shugart 1987). The larger territories observed in biking sites in our study suggests that habitat quality was poorer in these sites than in non-biking sites. Fragmentation and alteration of habitats in biking sites may have reduced the quality of these habitats for Golden-cheeked Warblers. For example, arthropod abundance may have been low within forest edges and near biking trails because of altered microclimate and vegetation structure (Jokimaki et al. 1998, Kilgo 2005). However, Davis and Leslie (2008) reported

TABLE 4. Foraging attack techniques ($\bar{x}$ ± SE) used by male Golden-cheeked Warblers at biking (n = 16) and non-biking (n = 21) sites near Austin and on Fort Hood, Texas during spring 2003.

Attack technique	Percent		P^a
	Biking	Non-biking	
Gleaning	57.4 ± 10.1	47.4 ± 8.9	0.555
Reaching	13.4 ± 7.2	29.3 ± 8.1	0.192
Hanging	3.1 ± 3.1	4.3 ± 4.3	0.823
Sally-striking	5.2 ± 3.6	1.1 ± 1.1	0.323
Sally-hovering	20.8 ± 8.6	16.1 ± 6.7	0.506
Flutter-chasing	0.0 ± 0.0	1.7 ± 1.2	0.232

[a] P-value from Kruskal-Wallis test with 1 df.

TABLE 5. Parental behavior ($\bar{x}$ ± SE) for female Golden-cheeked Warblers nesting in biking and non-biking sites near Austin and on Fort Hood, Texas during daylight hours in spring 2002 and 2003.

Parameter	Biking	Non-biking	P^a
Incubation stage[b]			
Incubation, %	67.40 ± 0.83	74.84 ± 0.93	0.105
No. of incubation bouts/day	17.98 ± 2.38	14.05 ± 2.12	0.355
Length of incubation bout, min	32.39 ± 6.86	38.44 ± 3.22	0.298
Early nestling stage[b]			
Brooding, %	36.59 ± 8.47	25.46 ± 7.42	0.257
No. of brooding bouts/day	16.82 ± 2.93	24.60 ± 8.06	0.345
Length of brooding bout, min	16.63 ± 5.72	12.60 ± 4.38	0.165
Feeding nestlings, %	7.46 ± 1.49	6.02 ± 0.93	0.852
No. feeding bouts/day	67.47 ± 17.07	79.65 ± 22.75	0.710
Length of feeding bout, min	1.38 ± 0.22	1.58 ± 0.48	0.850
Late nestling stage[b]			
Feeding nestlings, %	4.93 ± 1.08	4.25 ± 0.71	0.446
No. of feeding bouts/day	62.22 ± 9.91	76.24 ± 18.04	0.608
Length of feeding bout, min	1.19 ± 0.19	0.87 ± 0.20	0.440

[a] *P*-value from Kruskal-Wallis test with 1 df.
[b] Sample sizes for incubation stage, early nesting stage, and late nestling stage in biking and non-biking sites were 8 and 7, 7 and 8, and 9 and 11 nests, respectively.

that arthropod abundance from sweep-net samples of tree branches in biking and non-biking sites did not differ, and our study found no difference in foraging behaviors between biking and non-biking sites, which suggests that habitat quality was similar between biking and non-biking sites. Davis and Leslie (2008) did not distinguish between samples collected from forest edges or near biking trails and the impact of habitat fragmentation and alteration on arthropod abundance in biking sites is unknown.

Male Golden-cheeked Warblers in our study spent similar amounts of time engaged in diurnal behaviors in biking and non-biking sites. Nesting behaviors of female Golden-cheeked Warblers also did not differ between biking and non-biking sites. These observations suggest disturbance from mountain biking does not affect daily activity budgets of Golden-cheeked Warblers, but our direct observations of Golden-cheeked Warbler encounters with mountain bikers did show the birds were disturbed by bikers. During three of the four observed encounters with bikers, the bird flushed ≥20 m in response to the passing biker. Moreover, three of five nests abandoned at biking sites were <2 m from the trail, suggesting disturbance from mountain biking has a role in nest abandonment. We cannot conclude that direct disturbance from mountain biking is benign to nesting Golden-cheeked Warblers. Several studies have shown that direct human disturbance can alter activity budgets of birds (Stalmaster 1983, Kaiser and Fritzell 1984, Burger 1994, Mikola et al. 1994, Knapton et al. 2000). Our limited number of observations of direct encounters of Golden-cheeked Warblers and mountain bikers likely does not indicate that such encounters are rare, but rather, they are difficult to observe. We expect variations in biker behaviors (e.g., speed, group sizes, and silent vs. talking bikers) will elicit variable responses in warblers. These factors should be considered when evaluating the impact of mountain biking on Golden-cheeked Warblers.

Our estimate of nest success for Golden-cheeked Warblers in biking sites was lower than in non-biking sites (35 vs. 70%), but our nest success estimate for biking sites is comparable to other studies from Fort Hood (45% [Stake et al. 2004], 34% [Peak 2007], 40% [Reidy et al. 2009]) and Austin (40% [Reidy et al. 2009]). This lower nest success estimate in biking sites suggests those sites may provide lower quality nesting habitats for Golden-cheeked Warblers compared to non-biking sites. The nest success estimate for biking sites is still above the rate necessary to balance juvenile and adult mortality (25–30%; Donovan and Thompson 2001). Reidy et al. (2008) showed that Golden-cheeked Warblers can successfully reproduce in large protected urban sites, but they also suggested these habitats

may not be able to sustain productive populations if further disturbance in the landscape or breeding patch continues. This also appears to be the case for biking sites in our study, which are currently able to maintain viable populations of Golden-cheeked Warblers. Additional use, fragmentation, and alteration of these habitats could impact productivity by affecting densities of breeding adults, pairing success, or predator abundance which may result in these habitats becoming inadequate for sustaining viable populations (Reidy et al. 2008).

Reidy et al. (2009) suggested higher predator abundance and activity near edges contributed to low nest survival of Golden-cheeked Warblers near edges. The main predator of Golden-cheeked Warbler nests in our study was the Texas rat snake, which is a skilled tree climber (Pierce et al. 2008, Sperry et al. 2009) and major nest predator of Golden-cheeked Warblers (Stake et al. 2004, Reidy et al. 2008). Texas rat snakes prefer fragmented and edge habitats (Blouin-Demers and Weatherhead 2001, Sperry et al. 2009), and respond positively to increased edge and fragmentation (Sperry et al. 2009). Thus, it is likely that habitat fragmentation and alteration of biking sites by trails increased vulnerability of Golden-cheeked Warbler nests in those areas to predation by rat snakes and other edge-adapted predators. Sperry et al. (2009) suggested that Golden-cheeked Warbler nests that occurred in areas with many canopy openings, such as areas traversed by mountain bike trails, may be more at risk to rat snake predation.

The direct impact of mountain biking on Golden-cheeked Warblers may be minimal, but the indirect impact from fragmentation and alteration of habitats from mountain bike trails may reduce the quality of nesting habitat for Golden-cheeked Warblers. In particular, Golden-cheeked Warblers nesting in habitats fragmented and altered by mountain biking trails may be more vulnerable to nest predation (Reidy et al. 2009) and possibly encounter lower prey abundance (Jokimaki et al. 1998, Kilgo 2005). Conservation efforts that curtail construction of new mountain biking trails in Golden-cheeked Warbler habitat and reduce the amount of forest open edge habitat created by existing mountain biking trails should promote recovery objectives.

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SURVIVAL, SITE FIDELITY, AND POPULATION TRENDS OF AMERICAN KESTRELS WINTERING IN SOUTHWESTERN FLORIDA

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ABSTRACT.—The winter population ecology of American Kestrel (*Falco sparverius*), one of the most abundant and widely distributed raptors in North America, is poorly understood. We systematically searched a 225-km^2 area in Cape Coral, southwestern Florida, for American Kestrels during 14 winters (1 Dec–15 Mar, 1994–2008) to measure their annual apparent survival and to see if individuals returned to the same wintering area. We recaptured 101 of 2,958 banded kestrels during the study. We estimated annual apparent survival of 75% for males and 74% for females using a Cormack-Jolly-Seber model. These estimates are considerably higher than previous estimates for American Kestrels, but are similar to estimates reported for other species of *Falco*. Forty-six percent of the kestrels estimated to have survived were observed in the study area 1 year after recapture, based on year-specific color banding. All but six of 101 kestrels were recaptured within 1 km of where they were banded. Four of five kestrels banded as nestlings and subsequently recaptured in the study area were banded in southeastern Pennsylvania, suggesting migratory connectivity. Eighty percent of the kestrels trapped were females, but the proportion of females decreased annually ($-3 \pm 1\%$ per year). Overall, the population decreased by an average of $7 \pm 2\%$ per year. Recent land-use change accompanied by increased human density and suburban expansion may be causing the observed trends. *Received 29 October 2009. Accepted 9 March 2010.*

American Kestrels (*Falco sparverius*) occur in open habitats throughout most of North and South America (Smallwood and Bird 2002). The American Kestrel, historically abundant throughout most of its range, has declined significantly since the 1970s (Sullivan and Wood 2005, Farmer et al. 2008). Potential causes for this decline include West Nile virus, organophosphate poisoning, increased predation by growing populations of Cooper's Hawks (*Accipiter cooperii*), population declines of Northern Flickers (*Colaptes auratus*), a primary cavity nester; and land-use changes (Sullivan and Wood 2005, Farmer et al. 2006, Medica et al. 2007, Farmer et al. 2008).

American Kestrels are partial migrants that undertake leapfrog migration (Roest 1957, Smallwood and Bird 2002). Individuals breeding at northern latitudes are more likely to migrate and move greater distances than individuals breeding farther south (Goodrich and Smith 2008). Banding returns indicate that most individuals that migrate to southwestern Florida breed in the northeastern United States or in southeastern Canada (Layne 1982). Individuals or, more rarely, pairs of kestrels maintain areas of exclusive use during winter (Cade 1955, Mills 1975). Males and females use different habitats in winter with males occupying areas with more woody vegetation (Smallwood and Bird 2002). This may be the result of later-migrating males selecting suboptimal habitat left vacant by females (Smallwood 1988), or because larger females dominate smaller males (Ardia and Bildstein 1997).

Site fidelity by migratory birds can be advantageous because individuals benefit from being familiar with a previously occupied territory (Spaans 1977, Nichols et al. 1983). Familiarity with a territory likely allows for more efficient foraging and predator avoidance (Hinde 1956, Clarke et al. 1993, Yoder et al. 2004). Evidence supporting winter site fidelity in American Kestrels is limited to studies of small numbers of band recoveries and observation of uniquely marked individuals. Return rates of 19% (four of 21 individuals) and 17% (eight of 47) were reported at wintering sites in central Ohio (Mills 1975) and southern Texas (Bolen and Dorden 1980), respectively, for kestrels marked with patagial tags. Tabb (1977) reported a return rate of 2% (17 of 842) for kestrels banded at several sites in southern Florida, but that estimate is based entirely on recaptures because individuals could not be reliably identified without recapture. Several other species of raptors demonstrate winter site fidelity (Garrison and Bloom 1993, Harmata and Stahlecker 1993, Powers 1996).

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Moreover, satellite tracking has provided evidence for winter site fidelity by North American falcons, including Peregrine Falcon (*Falco peregrinus*) and Prairie Falcon (*F. mexicanus*), based on a small number of individuals (McGrady et al. 2002, Steenhof et al. 2005).

Survival estimates are essential for effective species' management and conservation (Crone 2001, Sandercock 2006). However, survival in the wild remains poorly known for the American Kestrel (Smallwood and Bird 2002). To date, two studies have estimated mortality rates using band recovery and territory occupancy (Roest 1957, Henny 1972), a technique that does not consider the probabilities of capture and detection biases and is further biased by territory vacancies that may not be the result of deaths of birds (Gould and Fuller 1995).

We report the results of a 14-year study of American Kestrels wintering in southwestern Florida. Specifically, we: (1) estimate annual apparent survival, (2) discuss a decrease in size of the observed population characterized by a decrease in number of females, (3) provide evidence for strong winter site fidelity, and (4) discuss evidence for migratory connectivity between winter territories in Florida and natal sites in the northeastern United States.

METHODS

Study Area.—We marked American Kestrels within ~275 km^2 containing 2,966 km of roads in the city of Cape Coral and adjacent Pine Island, west of Fort Myers, Lee County, Florida. The study site is on a peninsula along the Gulf of Mexico bordered to the east by the Caloosahatchee River and to the west by Matlacha Pass. Native cover includes slash pine (*Pinus elliottii*) woodlands and tidal marshes (Wesemann 1986, Millsap and Bear 2000). An extensive network of canals and roads was built in the area in the late 1950s (Bernard 1983, Zeiss 1983). The site now consists largely of single-family residences and unoccupied, but regularly mowed, lots (Millsap and Bear 2000). Parallel roads are ~100 m apart. The human population in 2000 was 102,286 (376.1/km^2). In 2006 it had grown 48% to 151,389 (556.7/km^2) (USCB 2009).

Data Collection.—BR and SR searched Cape Coral for American Kestrels each winter (1 Dec–15 Mar) for 14 years beginning in December 1994. Observers drove along each road in the study area at <25 km/hr while searching for kestrels, which often hunted from prominent perches and were easily observed (Bildstein and Collopy 1987). We surveyed each road once each winter and recorded male/female, location, and band color of all kestrels observed on our initial visit to each road.

We attempted to capture every kestrel observed by using a bal-chatri trap (25-cm-diameter, 7-cm-high) baited with two mice (*Mus musculus*) (Berger and Mueller 1959). Unless previously banded, captured kestrels were marked with a USGS aluminum band and a year-specific plastic, coil-style, color band (red, blue, white, yellow, black, or green), except for 1994–1995 and 1995–1996, when color bands were not used. Each color, except white, was used in 2 nonconsecutive years with bands being placed on different legs in different years. Wrap-around color bands were manufactured by Gey Band & Tag Company, Norristown, Pennsylvania, USA. A body-condition index was calculated for each captured bird by dividing the cube root of body mass by wing chord, which was used as a wing loading index for Merlins (*Falco columbarius*) by Temple (1972). If we were unable to capture a bird, we returned to the same site later in the season, usually in early March, and again attempted to trap it. However, observations of kestrels observed on a road after our initial survey of that road were not included in analyses. We indicated sites at which we banded or observed kestrels as the nearest intersection of roads. We obtained information on banding and recovery locations outside the Cape Coral study area from the Bird Banding Laboratory, USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. We considered recovered banded kestrels to have been found during the breeding season if they were found between 1 April and 31 August (*sensu* Smallwood and Bird 2002).

Statistical Analyses.—We estimated annual apparent survival (Φ) and capture probability (p) using recapture data with a Cormack-Jolly-Seber (CJS) model of mark-recapture in MARK 5.1 software (White and Burnham 1999). The model was based on a single study site with 14 recapture occasions (1995–2008). We used a single biological state, treating the age of all individuals as after-hatch-year. Our global model allowed apparent survival and capture probability to vary with year and male/female, as well as an interaction between those covariates. We retained all models for which ΔAIC_c was <2 and used model averaging to estimate parameters.

The initial capture and recapture sites for each recaptured bird were identified using ArcGIS (ESRI 2009). We tested for a difference between males and females in inter-capture distance, the distance between the site of original capture and the recapture site, using the Mann-Whitney *U*-test. We used Spearman's rank correlation to test for a relationship between inter-capture distance and years between captures and body-condition index at time of initial capture. We compared average annual capture success rate for marked and unmarked kestrels using a paired *t*-test.

Observed population was estimated as the number of kestrels observed on the initial visit to all roads. Effort did not vary among years and we used observed population as an index of true population size to compare among years. We used the natural logarithms of the female proportion of the population and the number of kestrels observed each year to estimate the change in the female proportion of the population, and the annual percent change in the observed population, respectively, using simple linear regression. All statistical analyses used SAS 9.1 (SAS Institute Inc. 2003). Tests were considered significant if $P < 0.05$. All error terms, except as noted, represent one standard error.

RESULTS

We captured 2,958 American Kestrels (211 ± 27/year), including 2,365 females, 592 males, and one individual for which we did not record gender. We recaptured 101 kestrels (80 females and 21 males) at least 9 months after their initial capture (Table 1). The mean time between banding and recapture was 2.8 ± 0.2 years (range = 11 months to 9 years). No bird was recaptured more than once. Each year, an average of 192 ± 56 individuals marked in previous years with year-specific color bands were observed, but these birds were difficult to recapture. Overall annual capture rates of unbanded kestrels were much higher than recapture rates for banded birds (61 ± 2% vs. 4 ± 1%; $t = 29.5$, $P < 0.001$).

We retained three models for apparent survival and recapture probability with $\Delta AIC_c < 2$ (combined Akaike weight, $w_i = 0.86$; Table 2). We estimated male apparent survival at 75 ± 5% and female apparent survival at 74 ± 4% based on model averaging. Overall, the year effect was not retained as a covariate affecting apparent survival, suggesting constant adult apparent survival during the 14 years of study. Recapture probability, as estimated with the CJS model, was low during the study period. It was greatest in 1995–1996 (5% for males and 4% for females), but remained between 1 and 3% for both males and females in every subsequent year until 2007–2008, when no kestrels were recaptured.

The proportion of females in the observed population (banded and unbanded) decreased by 3 ± 1% annually ($R^2 = 0.79$, $F = 38.0$, $P < 0.001$). Females comprised 86% of the population in the first 3 years of study and 64% of the population in the last 3 years. The total number of kestrels observed in the study area decreased an average of 7 ± 2% per year ($R^2 = 0.54$, $F = 11.6$, $P = 0.007$). The number of females observed decreased an average of 10 ± 2% per year ($R^2 = 0.63$, $F = 17.3$, $P = 0.002$; Fig. 1) and the number of males increased by 4 ± 1% per year ($R^2 = 0.37$, $F = 5.9$, $P = 0.035$).

For kestrels color banded in year n, we observed an average of 34 ± 1% in year $n + 1$, 18 ± 1% in year $n + 2$, and 9 ± 1% in year $n + 3$ (Fig. 2). Considering our estimate of annual apparent survival with a CJS model, we observed, in year $n + 1$, 46% of the kestrels banded in year n that were still alive in year $n + 1$ (Fig. 2).

The longest inter-capture distance that could have occurred within our study area was 32 km. Mean distance between initial and second capture for recaptured kestrels was 488 ± 102 m (range = 0 to 7,887 m). All but six birds recaptured were caught <1 km from the initial capture site, and 75% were recaptured within 423 m (Fig. 3). There was no difference in inter-capture distance between males and females ($U = 1{,}208$, $P = 0.26$), and inter-capture distance was not correlated with years between captures ($r_s = 0.083$, $P = 0.41$). Inter-capture distance and body-condition index at time of initial capture exhibited a nearly significant, weak correlation ($r_s = 0.19$, $P = 0.061$).

Twenty-five banded kestrels were observed outside the study area (Fig. 4). We recaptured five females in Cape Coral that had been banded as nestlings, four of which had been banded in eastern Pennsylvania and one of which had been banded in central Nova Scotia. We also recaptured two females that had been banded as adults, one in April in Connecticut and one in September on the Delmarva Peninsula, Virginia. Eighteen (11 females and 7 males) kestrels banded in Cape Coral were found dead outside the study area, including 13 (7 females and 6 males) that were

TABLE 1. Percent of American Kestrel cohorts recaptured each year after banding in Cape Coral, southwestern Florida. "*n*" indicates the number of kestrels banded each year. Subsequent columns indicate the percent (above) and number (below) recaptured each year after banding.

		Year of recapture												
Year	*n*	1995–1996	1996–1997	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002	2002–2003	2003–2004	2004–2005	2005–2006	2006–2007	2007–2008
1994–1995	207	3	<1	<1	0	1	0	1	<1	<1	0	0	0	0
		7	1	1	0	2	0	2	1	1	0	0	0	0
1995–1996	431		1	<1	0	<1	0	<1	0	0	0	0	0	0
			5	2	0	1	0	2	0	0	0	0	0	0
1996–1997	161			2	0	1	1	0	1	0	0	0	0	0
				4	0	2	1	0	1	0	0	0	0	0
1997–1998	224				0	1	2	<1	1	<1	0	0	0	0
					0	3	5	1	2	1	0	0	0	0
1998–1999	190					2	1	0	1	1	1	1	0	0
						4	2	0	1	1	1	1	0	0
1999–2000	404						2	0	<1	<1	<1	<1	<1	0
							8	0	1	2	1	2	1	0
2000–2001	195							1	1	1	1	1	0	0
								2	1	2	1	1	0	0
2001–2002	218								1	2	<1	<1	0	0
									3	4	1	1	0	0
2002–2003	274									1	1	1	0	0
										4	2	2	0	0
2003–2004	175										2	1	1	0
											3	2	1	0
2004–2005	124											0	0	0
												0	0	0
2005–2006	114												1	0
													1	0
2006–2007	102													0
														0
2007–2008	139													

TABLE 2. Models of apparent survival (Φ) and recapture probability (p) for recaptured American Kestrels (n = 101) in southwestern Florida for which $w_i > 0.10$. Both apparent survival and recapture probability were allowed to vary with year and sex, as well as an interaction between year and sex, in the global model. We tested all possible models nested within the global model. The best model not included in model averaging [Φ(sex)/p(year + sex)] had $\Delta AIC_c = 2.25$ and $w_i = 0.13$.

Model	AIC_c	ΔAIC_c	w_i	Parameters	Variance
Φ(.)/p(year)	1209.07	0.00	0.39	14	119.36
Φ(.)/p(year + sex)	1209.64	0.57	0.30	15	117.92
Φ(sex)/p(year)	1210.72	1.65	0.17	15	118.99

recovered during the breeding season, although we were not able to ascertain if kestrels died in breeding areas or as migrants. Kestrels recovered during the breeding season included five in Quebec, one in New Brunswick, one in Maine, two in New York, two in Pennsylvania, one in Delaware, and one in South Carolina. Kestrels recovered during the non-breeding season included one each in New Brunswick, Ontario, New York, North Carolina, and South Carolina. No birds captured in Cape Coral were recaptured outside the study area and reported to the Bird Banding Laboratory.

DISCUSSION

The annual apparent survival estimates of 75% for males and 74% for females are considerably higher than those reported by Roest (1957) and Henny (1972) (43 and 55%, respectively). Both of these studies relied on band recoveries from dead birds or nest-site occupancy to evaluate annual mortality rates. Their estimates of annual apparent survival are based on a time when direct persecution by humans (Bildstein 2008) may have resulted in greater mortality. At least 24% of the recovered kestrel bands reported by Roest (1957) came from birds killed by people. Human-caused mortality of kestrels reported in Henny (1972) ranged from 16% for 1958–1965 to 48% for 1925–1945. Our estimates are similar to estimates reported for other species of *Falco* in North America, including 75–89% for Prairie Falcons (Enderson 1969, Steenhof et al. 2006), 62% for Merlins (Lieske et al. 2000), and 79–93% for

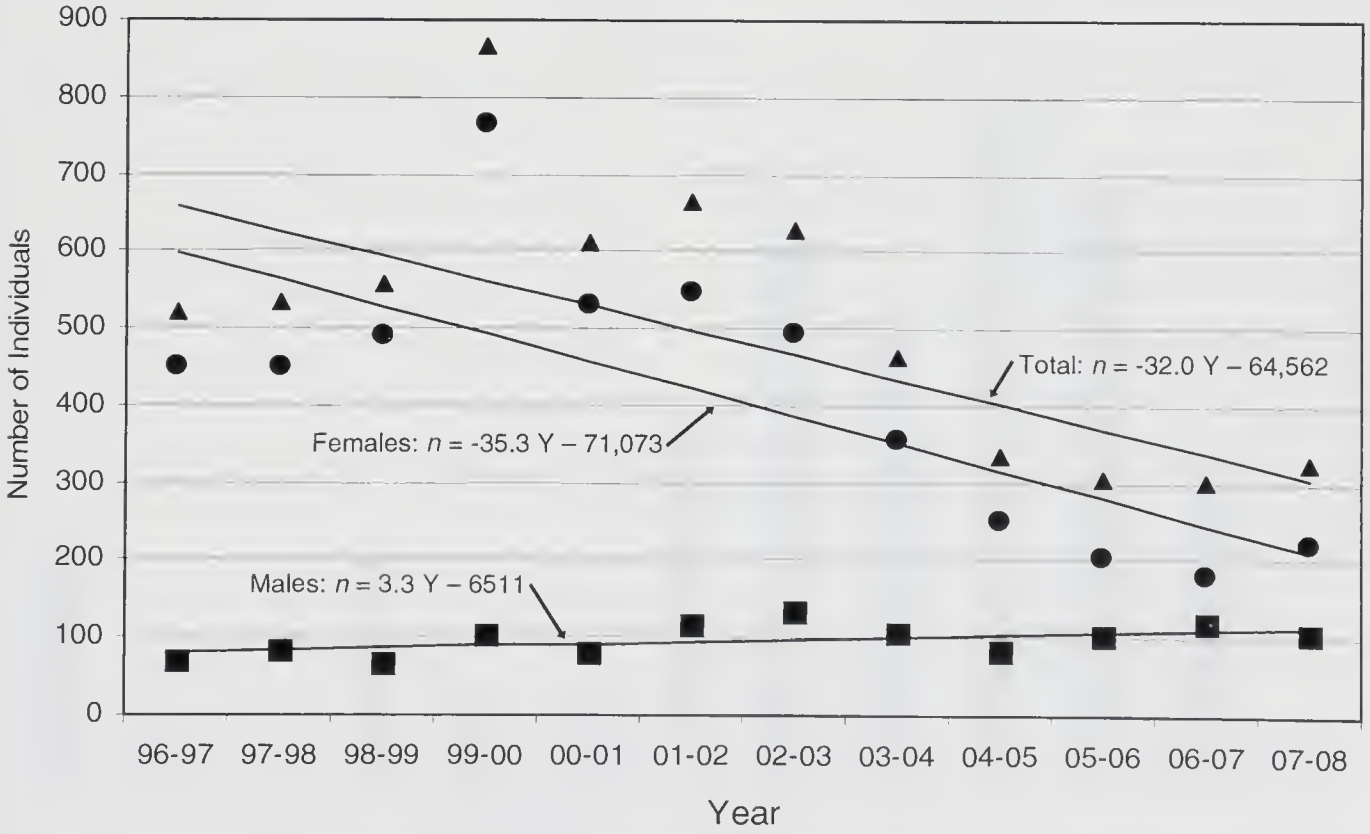

FIG. 1. Number of observations of female (circles), male (squares), and total (triangles) American Kestrels in Cape Coral, southwestern Florida, 1996–2008. "n" indicates number of kestrels and "Y" indicates the calendar year beginning in a winter season in the regression equations.

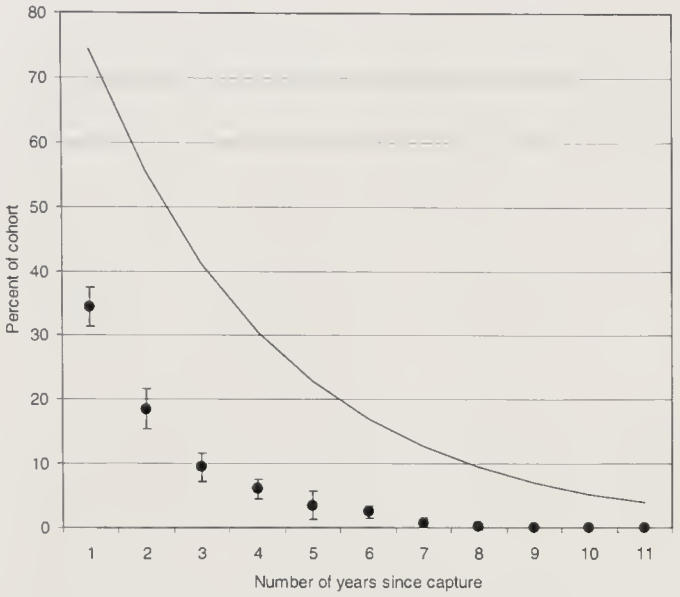

FIG. 2. Proportion of color-marked American Kestrel cohorts observed in Cape Coral, southwestern Florida and the estimated proportion surviving each year. Points indicate the average proportion of marked cohorts observed in the study area after each year. Vertical lines are 95% confidence intervals. The curve indicates the estimated surviving population based on annual adult apparent survival estimates from the CJS model in this study.

Peregrine Falcons (Court et al. 1989, Tordoff and Redig 1997). Survival estimates for Common Kestrels (*Falco tinnunculus*) in the United Kingdom were 80% for males and 66% for females (Dobson 1987). To our knowledge, this study reports the first estimates of annual apparent survival for American Kestrels using a CJS model.

We recognize use of year-specific color bands is not the most effective method to estimate annual apparent survival, recapture probability, and between-year inter-capture distances because it did not allow us to record individual encounter histories for kestrels that were not recaptured. Our estimate of apparent survival with the CJS model was based only on the 101 recaptured kestrels. We believe this estimate is reliable because it considers the low recapture probability.

The decline in the numbers of kestrels observed in the study area does not seem to be attributable to a decrease in adult survival over the study period as no year effect was retained in the models. However, the decrease in numbers of kestrels observed started in 2002, 3 years after discovery of West Nile virus in New York (Lanciotti et al. 1999). American Kestrels are susceptible to infection by West Nile virus (Komar et al. 2003) and exhibit symptoms that may decrease survival in wild birds (Nemeth et al. 2006). Ninety-five percent of tested American Kestrels breeding in Pennsylvania had antibodies indicating they had been exposed to the virus

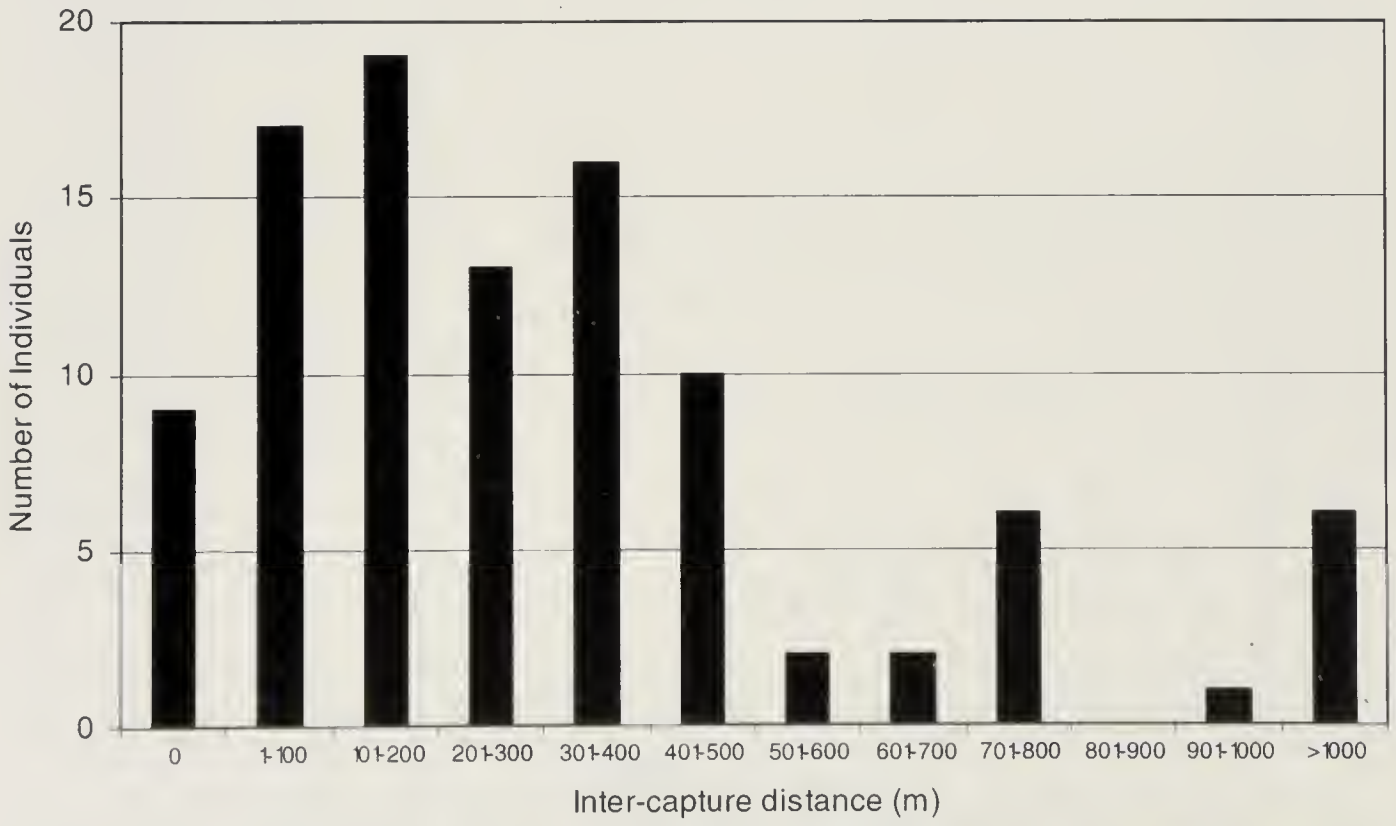

FIG. 3. Distances between capture and recapture sites between winter seasons for American Kestrels in Cape Coral, southwestern Florida. The greatest inter-capture distance was 7.9 km.

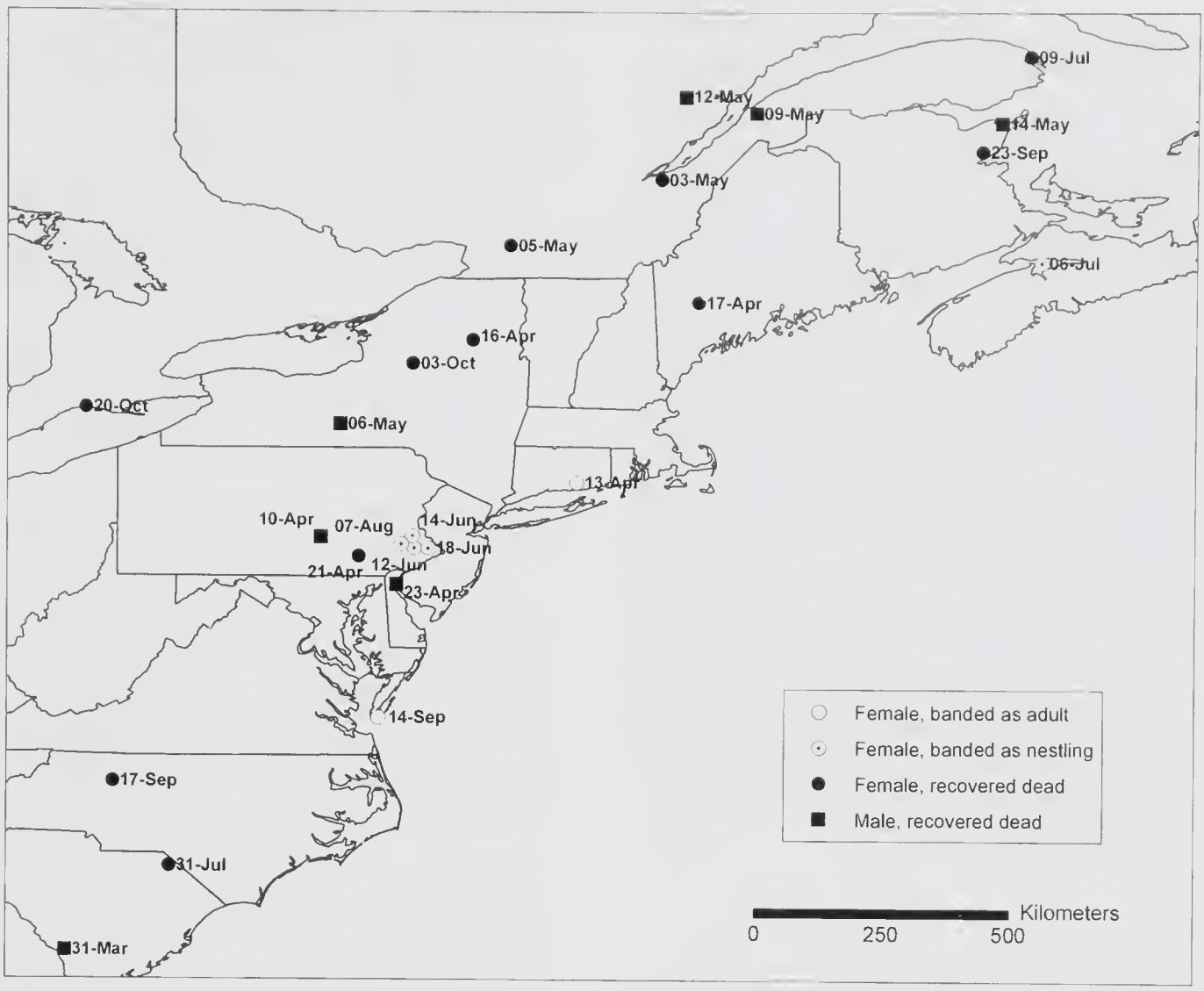

FIG. 4. Banding and band recovery sites for American Kestrels observed between 1 December and 15 March in Cape Coral, southwestern Florida. Males represented with squares and females with circles.

(Medica et al. 2007). The population decrease in our study area was characterized by a decrease in females. We believe this change in sex ratio could be due to land-use changes at the study site. Female kestrels occupy more open habitat in winter than males and, over the course of our study, land use in our study area shifted from open areas to more woody cover due to suburban development. The increase in number of males observed in the study area was relatively small compared to the decrease in the number of females observed. The observed increase in human population in the study area, combined with the suburban expansion of Cape Coral, has reduced the occurrence of good wintering habitat for kestrels. Those two factors seem to negatively affect the overall Cape Coral kestrel population as well as skew the sex ratio toward males.

American Kestrels wintering in Cape Coral, Florida exhibited strong winter site fidelity. Most kestrels that returned to the study area wintered a short distance (<1 km) from their previous wintering area, based on between-year inter-capture distances. The relatively large numbers of color-banded birds we saw, together with a small recapture rate, suggest the small number of recaptures was not due to emigration but rather to capture avoidance. Our observations of numerous color-banded kestrels in the area support strong winter site fidelity by American Kestrels. Our estimate of the proportion of birds observed in winters subsequent to capture is likely conservative due to loss of color bands (Nelson et al. 1980). Seven percent of the kestrels observed in the last year of our study (2007–2008) had an aluminum band and no color band. It is unlikely these kestrels had been banded in years when we did not use color bands (1994–1995 and 1995–1996) because we estimate that >96% of the kestrels banded in those years had already died by 2007–2008.

Four of five kestrels recaptured after being banded as nestlings outside the study area were banded within 42 km of each other in southeastern Pennsylvania, suggesting migratory connectivity in populations we studied. American Kestrels migrate singly or in small groups (Kerlinger et al. 1985), and juveniles migrate earlier than adults (Smallwood 1988, Mueller et al. 2000); thus, juveniles do not have the opportunity to follow adults on migration, as has been observed for some flocking migrants (Maransky and Bildstein 2001). Strong connectivity between natal and wintering areas has important conservation implications because a decrease in productivity in a local breeding population can drastically affect the population in wintering areas with which it is connected and vice versa. Recoveries of kestrels banded in the study area were distributed over a much wider range than were banding locations of nestlings recaptured in the study area, providing little evidence of connectivity between wintering and breeding areas for adults. We could not ascertain whether a recovered bird had died in its breeding area or as a migrant in most cases. We cannot clearly state there is a lack of migratory connectivity in adult kestrels.

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TEMPORAL AND SPATIAL SHIFTS IN HABITAT USE BY BLACK BRANT IMMEDIATELY FOLLOWING FLIGHTLESS MOLT

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ABSTRACT.—Each year thousands of Pacific Black Brant (*Branta bernicla nigricans*) undergo flightless wing molt in the Teshekpuk Lake Special Area (TLSA), Alaska, in two distinct habitats: inland, freshwater lakes and coastal, brackish wetlands. Brant lose body mass during wing molt and likely must add reserves upon regaining flight to help fuel their 2,500 km migration to autumn staging areas. We characterized movements and habitat use by Brant during post-molt (the period immediately following the recovery of flight) by (1) marking individual Brant with GPS (global positioning system) transmitters, and (2) conducting a series of replicate aerial surveys. Individuals molting in inland habitats promptly abandoned their molt wetland during the post-molt and moved into coastal habitats. Consequently, inland habitats were nearly deserted by early August when Brant had regained flight, a decrease of >5,000 individuals from the flightless period of early July. Conversely, coastal molting Brant largely remained in coastal habitats during the post-molt and many coastal wetlands were occupied by large flocks (>1,000 birds). Our results indicate that inland, freshwater wetlands were less suitable post-molt habitats for Brant, while coastal wetlands were preferred as they transitioned from flightless molt. The immediacy with which Brant vacated inland habitats upon regaining flight suggests that food may be limiting during molt and they are not selecting inland molt sites strictly for food resources, but rather a balance of factors including predator avoidance and acquisition of protein for feather growth. Our data clearly demonstrate that patterns of habitat use by Brant in the TLSA change over the course of the molt season, an important consideration for management of future resource development activities in this area. *Received 27 July 2009. Accepted 17 February 2010.*

Failed- and non-breeding individuals of many Northern Hemisphere goose species migrate to distantly-located molting areas to undertake a flightless wing molt (Hohman et al. 1992, Kjellen 1994). The flightless molt period imposes a number of constraints, including restricted ability to escape predators or access unused habitats and food sources (Fox and Kahlert 2000, Kahlert 2006). Growth of new flight feathers requires intake of certain nutrients essential to feather development, especially proteins and sulfur-containing amino acids (Murphy and King 1984, Sedinger 1984, Heitmeyer 1988, Fox and Kahlert 1999). Fox and Kahlert (2005) suggested that geese alleviate these constraints by choosing wing molting habitats that balance low predation risk with food supplies high in protein and energy. The constraints of the flightless period are immediately relaxed upon regaining flight, however, and habitat attributes necessary for molting, including open-water escape areas or availability of nutrients for feather growth, may no longer drive habitat selection.

Northern Hemisphere geese migrate soon after completing their molt, often traversing considerable distances from arctic molting sites to more southerly staging and wintering areas (Hohman et al. 1992). However, because the flightless wing molt is an energetically costly event and geese often lose considerable body mass during the molt (Williams and Kendeigh 1982, Taylor 1993, Fox and Kahlert 2005, Portugal et al. 2007), geese likely need to accumulate new fat reserves to fuel their forthcoming migration. Thus, post-molt habitats may be chosen largely for food availability and, when a molt site offers sufficient food availability for birds to build reserves, individuals may opt to stay at that site beyond the time at which flight was recovered. Conversely, abrupt abandonment of a molt site following recovery of flight may suggest food is limiting and alternate sites offer superior food supplies, conferring a selective advantage to birds that change sites.

Each year, thousands of Pacific Black Brant (*Branta bernicla nigricans*; hereafter Brant) migrate to the Teshekpuk Lake Special Area (TLSA), on the Arctic Coastal Plain of Alaska, where they undergo flightless wing molt (Derksen et al. 1982, Taylor 1995). TLSA and surrounding areas provide Brant with a choice between two distinct molting habitats in close proximity: coastal, brackish wetlands or inland, freshwater wetlands (Flint et al. 2008). Each habitat offers different plant species as potential forage for molting Brant, as well as different types of open-water escape habitat (Markon and Derksen 1994,

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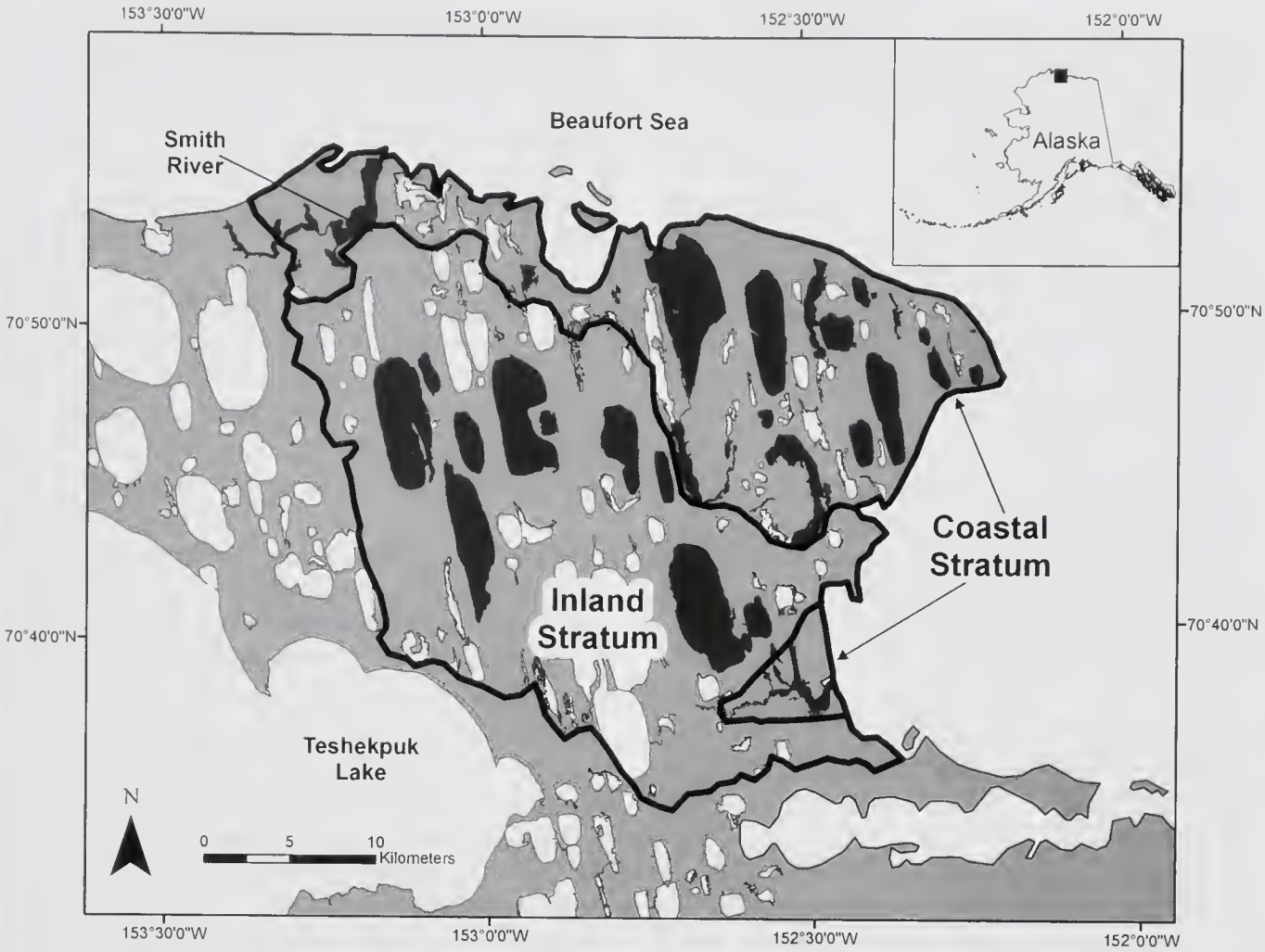

FIG. 1. Molting goose region of the Teshekpuk Lake Special Area, Alaska, during 2006–2008. Lakes at which Brant were aerially surveyed are darkened and strata boundaries are depicted with bold lines.

Flint et al. 2008). We examined the post-molt ecology of Brant in the TLSA to better understand the potential differences in food availability and quality between coastal versus inland habitats, as well as preference of Brant for each habitat type following the recovery of flight. We used a combination of population-level aerial surveys and individuals marked with GPS (global positioning system) transmitters to examine changes in Brant distribution from molt to post-molt, probability of remaining on a molt site following recovery of flight, and types of habitats used post-molt.

METHODS

Classification of Coastal versus Inland Molter.—The TLSA is characterized by tundra vegetation, continuous permafrost, and large permafrost thaw lakes (Markon and Derksen 1994, Jorgensen et al. 2006). Flightless molting Brant occur primarily in the northeast section (Fig. 1) and are primarily subadults, non-breeders, and failed-breeders associated with breeding colonies in Alaska, Russia, and western Canada (Bollinger and Derksen 1996). Flint et al. (2008) divided the TLSA molting area into three strata based on distinct vegetative and landscape characteristics. The majority of our research was conducted in strata two (inland stratum) and three (coastal stratum; Fig. 1). The coastal stratum is characterized by the occurrence of saltwater intrusion, elevations <1.5 m, and salt-tolerant plant communities, while the inland stratum has a lack of saltwater intrusion, slightly greater elevations (≤ 4 m), and predominantly freshwater plant communities. Brant marked with transmitters were classified as either inland or coastal molters depending upon the stratum in which they molted. Additionally, some transmitter-marked Brant molted in areas near the TLSA, but outside the stratum boundaries. This latter group molted solely in coastal habitats and is included in the coastal molter classification.

GPS Transmitters.—Our first method for characterizing movements and habitat use of Brant during the post-molt was through use of GPS

transmitters. We captured female Brant from nesting colonies on the Arctic Coastal Plain of Alaska, between Barrow (71° 18′ N, 156° 44′ W) and the Colville River Delta (70° 25′ N, 150° 23′ W), during two summers (2007–2008). We captured birds on nests using spring-loaded bow traps (Sayler 1962) and marked them with GPS transmitters. We removed eggs from nests of captured females changing their status to failed breeder and significantly increasing the likelihood they would migrate to the TLSA to undergo flightless wing molt. We marked 39 Brant from 11 to 17 June 2007 and 39 Brant from 12 to 20 June 2008. We experienced high rates of transmitter failure in both years of our study as verified via incidental recaptures of Brant with failed transmitters, recovery of defective transmitters from hunter-harvested individuals, and sudden loss of transmitter signals from flightless individuals (i.e., birds that could not move from our reception range). Thus, missing transmitters are largely attributable to transmitter failure rather than molt migration from our study area (Lewis and Flint 2008).

GPS transmitters were externally affixed between the shoulder blades of captured Brant via dual subcutaneous anchors, following Lewis and Flint (2008). We used two models of GPS transmitters in 2007 that differed only in power source: solar (n = 19) and battery powered (n = 20). All 39 GPS transmitters used in 2008 were battery-powered. Estimated transmitter life was 45–60 days for battery-powered transmitters and 45+ days for solar models. GPS transmitters were programmed to collect and store a location every 6 hrs and offload all stored locations via a daily VHF radio transmission. Offloaded data were collected weekly from fixed-wing aircraft equipped with wing-mounted two-element yagi antennas. Data were downloaded using an HR2600 receiver produced by HABIT Research (Victoria, BC, Canada).

Aerial Surveys.—Aerial surveys, our second method for characterizing Brant movements and habitat use, encompassed most of the molting Brant population in the TLSA. We conducted replicate aerial surveys of 33 selected lakes within the TLSA during summers 2006–2008 (Fig. 1). The initial survey was during the first week of July and repeated on a weekly basis for 6 weeks, encompassing the core molting period of Brant (Derksen et al. 1982). The survey protocol followed that used by the U.S. Fish and Wildlife Service (USFWS) in their annual mid-July survey of molting geese in the TLSA as described by Flint et al. (2008). This protocol assumes that detection rate and observer error are constant on all surveys. We used the USFWS survey data from 1996 to 2005 to select the subsample of lakes for our repeated survey, choosing only lakes that were used by >200 Brant in ≥3 years. This resulted in a subsample of 33 lakes which typically contained >90% of the molting Brant counted in these years. All surveyed lakes were within the boundaries of either the inland or coastal stratum and were classified accordingly (Flint et al. 2008).

Statistical Analyses.—We calculated two variables using data from our birds marked with GPS transmitters to explore Brant post-molt ecology: probability of molt site abandonment and distance from coastline. Both variables are time-dependent, being measured in relation to time since onset of molt, and thus required that start date of molt be known. We used an algorithm, which assumed movement rates of Brant are significantly reduced during the flightless molt, to estimate each individual's start date of molt. The algorithm, described by Lewis et al. (2010), identified the date at which movement rates distinctly changed, allowing us to objectively define a precise date of molt initiation for each of our transmitter-marked birds. We did not use this algorithm to estimate the end date of molt because many individuals did not increase their movement rates or move among wetlands despite presumably regaining flight. We used estimates from previous Brant research in the TLSA which found that partial flight is regained ~23 days after shedding of flight feathers (Taylor 1995). We assumed for all analyses that Brant had regained partial flight by 23 days from the onset of flightlessness.

We quantified timing of molt site abandonment for each of our transmitter-marked individuals. Most wetlands used during molt are separated by wide stretches of upland tundra which are essentially impassable to flightless Brant; thus, individuals are often confined to one wetland, or interconnected wetlands, until flight is regained. Individuals were assigned a primary molt wetland from the time molt started, as calculated by our molt algorithm, and their daily status classified as "present" until they moved to a different, unconnected wetland, at which point their status was classified as "abandoned". This exercise produced a binary variable for each of our

transmitter-marked individuals, where each day since the onset of molt was classified as either present or abandoned. We used this binary variable in Kaplan-Meier survival models to estimate the daily probability of molt site abandonment for coastal and inland molters. The Kaplan-Meier analysis produced separate probability curves for coastal and inland molters with each curve plotting the probability that Brant remained on their primary molt wetland versus time since onset of molt. We used a log-rank test of equality to examine the null hypothesis (α = 0.05) that there was no difference in probability curves of coastal versus inland molters (Pollock et al. 1989).

We modeled the distance from coastline in relation to time since onset of molt to examine if coastal versus inland molters differed in their post-molt habitat use. We fit a series of general linear models (GLM) to describe the shape of time trends for the explanatory variable of 'distance from coast'. Models examined included intercept, linear, quadratic, and cubic time function with the best-fitting model selected using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). The start of molt was defined as time zero with time (hrs) of all subsequent GPS locations added onto zero and all prior GPS locations subtracted from zero. The cubic function was the best-fitting time model (ΔAIC = 0) and all other models had a ΔAIC < 4.0. Thus, using 'distance from coast' as our explanatory variable, we next fit a series of general linear mixed models in which the cubic time function was included in all models. We used mixed models to account for repeated measures of individuals marked with transmitters by including subject as a random effect (Littell et al. 2000). The mixed models included the response variable 'habitat', defined as either coastal or inland depending upon the habitat strata in which each individual molted. The model set included a time only model, habitat as an additive variable with time, or all combinations of habitat by time interactions for a total of nine models. The best-fitting model was selected using ΔAIC and the null model (intercept-only) was compared against each model to assess model fit (Burnham and Anderson 2002).

We examined the spatial distribution of Brant across strata by summarizing each aerial survey as the ratio of Brant counted inland to Brant counted coastally and used this ratio as our response variable to fit a candidate set of GLMs. We used

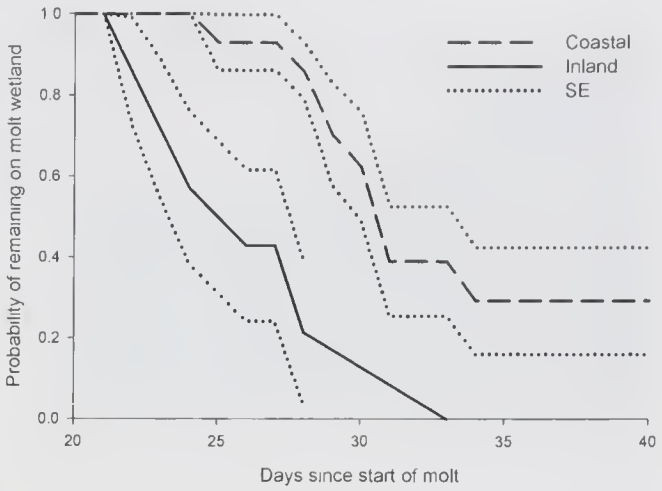

FIG. 2. The probability individuals remained on their molt wetland by number of days since start of molt for Brant marked with GPS transmitters which molted at coastal versus inland wetlands, Teshekpuk Lake Special Area, Alaska, during 2007–2008. Brant typically regain flight 23–24 days after onset of molt.

year (2006, 2007, 2008) and Julian date of each survey as our explanatory variables, and our candidate model set consisted of single variable models, the additive model, the interaction model, and the intercept-only null model for a total of five models. Akaike's information Criterion (AIC_c), adjusted for small sample size, was calculated for each model in the candidate set, ΔAIC_c and AIC weights (w_i) were used to infer the relative support of each model, and the null model (intercept-only) was compared against each model to assess model fit. All analyses were performed using SAS Version 9.1 statistical software (SAS Institute 2003) and descriptive statistics are presented as mean ± SE.

RESULTS

GPS transmitters on 23 Brant functioned for ≥23 days from onset of flightlessness allowing us to examine Brant behavior as they transitioned from their flightless molt. Sixteen of these 23 birds were classified as coastal molters and seven as inland molters. The probability that an individual remained on its molt wetland on a given day was significantly different for coastal versus inland molters (log-rank test, χ^2 = 7.73, df = 1, P = 0.005), as inland molters abandoned their molt site sooner than coastal molters (Fig. 2). Abandonment of molt sites by inland molters began 22 days after molt initiation and the probability of remaining at their molt site was 21% at 28 days. Abandonment of molt sites by coastal molters began 25 days after molt initiation

TABLE 1. Candidate general linear mixed models evaluating variation in distance from coast (m) for Brant with GPS transmitters in the Teshekpuk Lake Special Area, Alaska, 2007–2008. The explanatory variables are time (t), included as a cubic function ($t + t^2 + t^3$) in all models, and habitat (h) defined as coastal or inland. Models are listed in order of ΔAIC.

Model	Parameters	Log-likelihood	ΔAIC	w_i
$h + t + ht + t^2 + ht^2 + t^3$	10	−3,5927.29	0	0.37
$h + t + ht + t^2 + t^3 + ht^3$	10	−3,5927.34	0.09	0.36
$h + t + ht + t^2 + ht^2 + t^3 + ht^3$	11	−3,5926.85	1.11	0.21
$h + t + t^2 + t^3 + ht^3$	9	−3,5930.88	5.17	0.03
$h + t + t^2 + ht^2 + t^3$	9	−3,5931.61	6.65	0.01
$h + t + t^2 + ht^2 + t^3 + ht^3$	10	−3,5930.83	7.09	0.01
$h + t + ht + t^2 + t^3$	9	−3,5937.37	18.16	0.00
$h + t + t^2 + t^3$	8	−3,5938.63	18.67	0.00
$t + t^2 + t^3$	7	−3,5947.15	33.71	0.00

and the probability of remaining at their molt site was 86% at 28 days.

The best-fitting model (ΔAIC = 0) to explain distance from the coast for Brant marked with GPS transmitters contained the explanatory variable of habitat, defined as coastal or inland molter, in the habitat*time (*ht*) and habitat*time*time (ht^2) terms of the cubic function (Table 1). Two other models also received substantial support (ΔAIC ≤ 2): the model with habitat in the *ht* and ht^3 terms and the model with habitat in all three terms of the cubic time function (Table 1). The null model, in which the habitat variable was not included, received no empirical support indicating that inclusion of habitat explains a significant amount of variation in distance to coast (Table 1). Plots of predicted values for each of the three well-supported models indicate they differ only at the extreme tails of the cubic functions. The biological inference for each of the three well-supported models is identical and we used model-averaged estimates, based on the three top models, for all further inference. Model-averaged parameter estimates (Table 2) indicate that by 23 days after initiation of molt, when many Brant have regained flight, inland molting Brant promptly moved into coastal habitats, while coastal molting Brant remained in coastal habitats (Fig. 3). Inland and coastal molters were at similar distances from the coast before the onset of molt and were ~8 and 2 km from the coast during the flightless molt, respectively (Fig. 3).

The best-fitting model ($\Delta AIC_c = 0$) to explain the proportion of Brant per habitat strata, as counted from aerial surveys, contained only Julian date as a response variable (Table 3). The additive model containing year and Julian date received moderate support, although its w_i was low relative to the top model (Table 3). All other models, including the null model, had ΔAIC_c values >20. These results indicate the distribution of Brant across habitat strata was strongly influenced by Julian date. The proportion of Brant in the coastal stratum increased by date beginning in mid to late

TABLE 2. Weighted parameter estimates and unconditional standard error (SE) for general linear mixed models evaluating variation in distance from coast (m) for Brant with GPS transmitters in the Teshekpuk Lake Special Area, Alaska, 2007–2008.

Explanatory variable[a]	Parameter estimate	Unconditional SE
Intercept	7,572.67	947.77
Habitat	−5,350.29	1,074.16
Time	3.48	1.69
Habitat*Time	−5.19	1.88
$Time^2$	$-1.48*10^{-3}$	$5.87*10^{-3}$
Habitat*$Time^2$	$6.21*10^{-3}$	$3.98*10^{-3}$
$Time^3$	$-3.47*10^{-6}$	$6.81*10^{-6}$
Habitat*$Time^3$	$5.47*10^{-6}$	$3.67*10^{-6}$

[a] Habitat is a categorical variable (coastal or inland) with inland as the reference value.

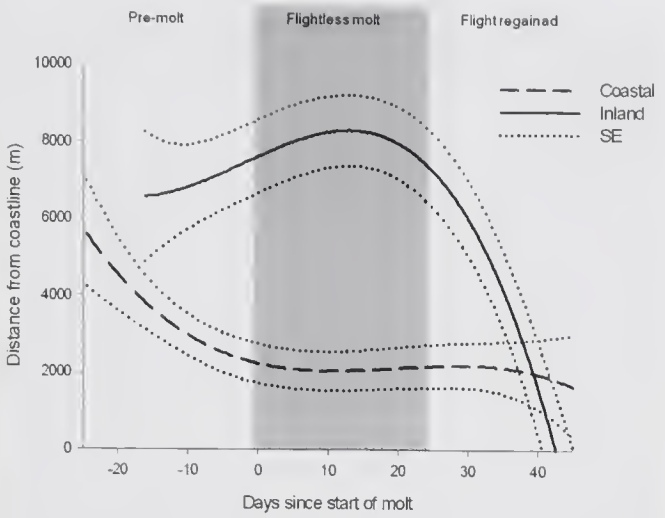

FIG. 3. Model averaged estimate of distance from coastline (m) by days since start of molt for Brant marked with GPS transmitters which molted at coastal versus inland wetlands, Teshekpuk Lake Special Area, Alaska, during 2007–2008.

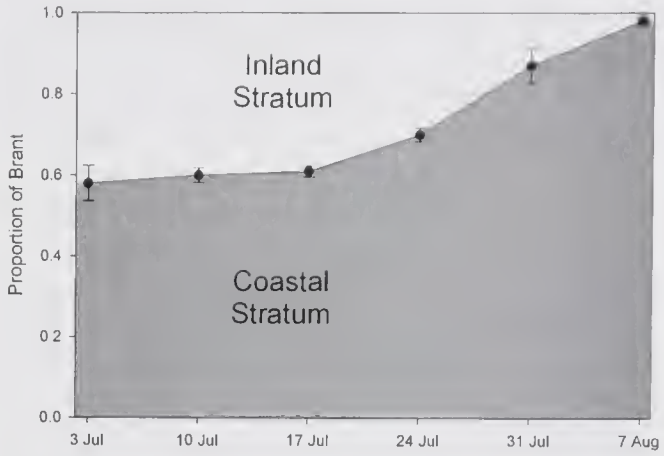

FIG. 4. The proportion of Brant in coastal versus inland strata based on aerial surveys, Teshekpuk Lake Special Area, Alaska, conducted during July–early August, 2006–2008. Aerial surveys were conducted six times per year with each survey separated by ~1 week. Weekly surveys are summarized across years, producing weekly means ± SE.

July as they began to regain flight (Fig. 4). This pattern of movement into the coastal stratum did not differ across years or by the interaction of year*date. Most Brant had regained flight by early August and >90% were in the coastal stratum, a 30% increase from the flightless molt period (Fig. 4). The increased proportion of Brant in the coastal stratum did not result from inland molters leaving the TLSA altogether. Rather, the number of birds in the coastal stratum increased or remained constant during late July, despite some coastal molters leaving the area. Thus, many inland molters moved into coastal stratum habitats upon regaining flight, similar to the pattern observed for our individuals marked with transmitters. Aerial surveys, however, demonstrated this pattern for much larger numbers of Brant (>15,000 annually) and over a larger spatial area.

Post-molt habitat use varied among wetlands within the coastal stratum with some being completely abandoned by Brant during the post-molt while others experienced increases of hundreds to thousands of Brant. Numbers of Brant either increased or remained stable at 40% of the 22 coastal wetlands for which sufficient aerial survey data were available during the post-molt period; conversely, post-molt Brant numbers decreased significantly at all nine inland stratum wetlands surveyed. The coastal wetland complex at the Smith River (Fig. 1) was particularly important, supporting >5,000 Brant annually during the post-molt, an increase of 2,000–3,000 birds above the wetland's average annual molting population.

TABLE 3. Candidate general linear models evaluating variation in ratio of Brant counted inland versus those counted coastally during aerial surveys conducted in the Teshekpuk Lake Special Area, Alaska, 2006 to 2008. Models are listed in order of ΔAIC.

Model	Parameters	R^2	ΔAIC	w_i
Julian date	3	0.86	0	0.68
Julian date + Year	5	0.90	1.53	0.32
Julian date + Year + Julian date*Year	8	0.91	21.41	0
Null	2	0	28.00	0
Year	4	0.02	34.38	0

DISCUSSION

Brant regain flight when their primaries reach 70–75% of their full-grown length, which typically occurs 23–24 days after onset of molt (Taylor 1995). Using this timeline, we found that individuals molting in inland, freshwater habitats abandoned their molt site almost immediately upon regaining flight, moving almost exclusively into coastal habitats. Inland wetlands were nearly abandoned by early August, a decrease of >5,000 individuals from the flightless period of early July, and the only remaining individuals were likely those which had yet to attain flight.

Conversely, Brant molting in coastal habitats continued to reside on their molt wetlands for several days after regaining flight and did not switch habitats during the post-molt, remaining within coastal habitats. Many coastal wetlands were occupied by large flocks (>1,000 birds) of flying Brant during the post-molt. Our results indicate Brant almost universally prefer coastal habitats immediately following recovery of flight and inland, freshwater wetlands and lakes are less suitable post-molt habitats. Our results also corroborate earlier research from the 1980s, in which a small sample (n = 18) of radio-marked Brant moved from inland to coastal sites during the post-molt period (Jensen 1990). This suggests the post-molt patterns observed in our study have persisted over a timescale spanning no less than multiple decades.

Brant molting in inland habitats chose to leave their molt site sooner than those molting coastally, but the differential timing of molt site abandonment could alternatively be explained by differential molt durations between the two habitat types. Habitat-specific factors, such as food quality, competition for resources, or presence of other stressors may influence the rate of feather growth and, by extension, the duration of molt (Hahn et al. 1992, Romero et al. 2005). Citril Finches (*Carduelis citrinella*) in higher quality habitats molted more rapidly than those in low quality habitats, despite the two habitats being only 5 km apart (Borras et al. 2004). Similarly, the longer residency of Brant at coastal molt sites may be due to hypothetically poorer habitat quality at these sites, rather than individuals choosing to remain past the recovery of flight. We cannot completely discount this alternative hypothesis, but we find it unlikely that quality differences between coastal versus inland habitats would shift molt durations to the extent that explains our observed differences in timing of molt site abandonment. Abandonment of coastal molt sites lagged that of inland sites by ≥5 days, a pronounced difference for a species that averages 23 days to regain flight, and >50% of coastal-molting individuals had not moved by day 30. The majority of Brant molted coastally and inland molting Brant promptly moved to coastal habitats following cessation of molt, suggesting that coastal habitat quality is at least equivalent with inland habitats, if not superior. Overall, the patterns of post-molt movements and habitat use by Brant would not seem to support the hypothesis that variation in time spent at molting locations is negatively associated with habitat quality.

Adult Brant collected in the TLSA from 1988 to 1989 lost >20% of their body mass and >80% of their lipid reserves during the flightless wing molt, completing molt with lipid reserves comprising only 2–4% of body mass (Taylor 1993). More recent research (2005–2007) also documented considerable body mass losses for molting Brant, although rates of mass loss were slower than during 1988–1989 (PLF, unpubl. data). Given significant declines in body mass and lipid reserves, molting Brant must regain body reserves during the post-molt period to fuel their forthcoming 2,500 km migration to their primary autumn staging area at Izembek Lagoon, Alaska (Vangilder et al. 1986, Dau 1992, Reed et al. 1998). Post-molt distributions of Brant are likely driven by availability and quality of food resources, and the unidirectional movement of Brant from inland habitats suggests that inland food resources are less able to fulfill post-molt requirements than coastal resources. The immediacy with which Brant vacated inland stratum habitats upon regaining flight also suggests food is limiting during molt, potentially due in part to Brant grazing pressure, and Brant are not selecting inland molt sites strictly for food resources. Brant are likely selecting inland molt sites for a balance of factors which includes protein supplies for feather growth and large open-water areas for predator avoidance (Fox and Kahlert 2005).

The sedge *Carex subspathacea* and grass *Puccinellia phyragnodes* grow in saline-influenced tundra habitats (Markon and Derksen 1994) and are preferred forage items of Brant across the arctic and subarctic (Sedinger et al. 2001, Person et al. 2003). These plant species in the coastal habitats of the TLSA often occur as 'grazing lawns', which are areas of high density plant growth created by frequent goose grazing (Person et al. 2003). Grazing lawns typically experience short-term reductions in food abundance due to the immediate effects of grazing, but their long-term maintenance requires frequent grazing to create positive feedbacks of increased plant growth rates and nutrient content (Ruess et al. 1997, Person et al. 2003). The nitrogen recycled through goose feces contributes to the salinity tolerance of grazing lawns (Ruess et al. 1997). The pronounced post-molt shift of Brant into coastal habitats likely contributes to mainte-

nance and expansion of grazing lawns, increasing coastal food availability and further prompting Brant to exploit coastal habitats. The coastal plants grazed by Brant also have lower carbon to nitrogen ratios (C:N), the main index of food quality for geese (Riddington et al. 1997, Hassall et al. 2001), than the common inland stratum forage plants of *Carex aquatilis* and *Deschampsia caespitosa* (JAS, unpubl. data). Brant, because of their small body size and correspondingly small digestive tract, have high food passage rates and require high quality foods from which nutrients can be quickly extracted (Prop and Vulink 1992, Sedinger 1997). Coastal areas in the TLSA are heavily influenced by summer fogs, which locally reduce air temperature and solar exposure, potentially delaying plant phenology (Post and Stenseth 1999, Menzel et al. 2006). Plant quality decreases as the arctic summer progresses (i.e., C:N temporally increases), and delayed phenology in coastal areas would result in higher quality forage plants during the late season post-molt period (Crawley 1983, Van der Wal et al. 2000). The combination of higher quality plant species and delayed plant phenology in coastal habitats may also be important factors contributing to the post-molt shift of Brant into coastal habitats.

The TLSA also supports large numbers of molting Greater White-fronted (*Anser albifrons*), Canada (*Branta canadensis*), Cackling (*B. hutchinsii*), and Lesser Snow (*Chen caerulescens caerulescens*) geese along with Brant. The number of molting geese counted in the TLSA in recent years has ranged from 70,000 to 90,000, collectively making this one of the most significant goose molting areas in the circumpolar arctic (Flint et al. 2008). The TLSA is currently designated for future leasing for oil and gas extraction (2008 Northeast NPR-A Record of Decision; available at http://www.blm.gov/ak/st/en/prog/energy/oil_gas/npra.html). Planning to minimize the effects of development of molting areas on Brant populations will require a clear understanding of patterns of habitat use and how patterns may change seasonally. The only data currently available to assess patterns of habitat use of Brant in the TLSA comes from a single annual survey conducted during the peak flightless period in mid-July (Flint et al. 2008). These survey data are not suited to describing intra-annual patterns of habitat use, such as the post-molt habitat shifts we describe. Our data clearly demonstrate that patterns of habitat use by Brant in the TLSA change over the course of the molt season, and that future management and development decisions must consider seasonal variation in distributions of Brant.

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ARTHROPOD FORAGING BY A SOUTHEASTERN ARIZONA HUMMINGBIRD GUILD

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ABSTRACT.—We tested the hypothesis that foraging for arthropods may be a viable source of energy when hummingbirds are competitively excluded from sources of nectar. We hypothesized that the Magnificent Hummingbird (*Eugenes fulgens*) relies more upon arthropods than the Blue-throated Hummingbird (*Lampornis clemenciae*) or Black-chinned Hummingbird (*Archilochus alexandri*) in southeastern Arizona. We were unable to quantify arthropod foraging by *A. alexandri*, but measured frequent arthropod foraging by both *E. fulgens* and *L. clemenciae*. *E. fulgens* engaged in more aerial flycatching than *L. clemenciae*, and their rate of flycatching attempts was higher than by *L. clemenciae*. Analysis of gut contents showed that *E. fulgens* consumes the greatest diversity of arthropods. Respiratory quotient measurements indicated *E. fulgens* catabolized a greater amount of fat/protein than the other species. Gut morphology of *E. fulgens* does not appear to differ from other hummingbirds suggesting hummingbirds in general may have the ability to use arthropods as an alternative energy source when access to floral energy is restricted. Our data are consistent with the hypothesis that the diet of *E. fulgens* includes more arthropods than other species with which they compete. *Received 10 November 2009. Accepted 3 February 2010.*

Floral nectar has been assumed to be the primary energy resource of hummingbirds. This is reasonable from both ecological and physiological perspectives when one considers that many aspects of hummingbird and floral natural history are intertwined (Feinsinger 1983, Stiles 1995), and that sugars in floral nectar are quickly and easily digested. It is also known that hummingbirds supplement their diets with small arthropods as floral nectar lacks many important nutrients (Baker 1977). However, arthropods are generally considered to be of little energetic importance for hummingbirds (Wolf and Hainsworth 1971).

Hummingbirds often spend <10% of their day foraging for arthropods when nectar is in sufficient supply (Gass and Montgomerie 1981). There is evidence that arthropod consumption increases during specific periods of the natural cycle of hummingbirds such as during reproduction, specifically by nesting females (Murphy 1996), and during periods of low nectar availability (Chavez-Ramirez and Dowd 1992). Time spent on other activities, including nectar foraging, is likely reduced when time spent foraging for arthropods increases (Chavez-Ramirez and Dowd 1992). Stiles (1995) argued that hummingbirds acquire a meaningful amount of energy from consumption of arthropods, which would be needed to meet energy demands when nectar intake is reduced. This is not difficult to imagine since arthropods have high energy content (Weathers and Sullivan 1989) and appear to be fully digested in a hummingbird's digestive tract (Remsen et al. 1986).

We know of no studies that examined the possibility that hummingbirds might use arthropods when excluded from a nectar source because of local social interactions. For example, an aggressive dominant species could restrict access of subordinate species to clumps of flowers contained within its territory forcing the subordinate species to seek alternative energy sources (Young 1971). This may reduce the energetic impact of competition if the subordinate could use arthropods as a primary energy source. This attribute would provide ecological separation between competitors so they can coexist (Rosenzweig 1985, Sandlin 2000b) in areas that do not provide abundant nectar resources (Brown et al. 1978).

Eugenes fulgens (Magnificent Hummingbird) is a member of a three-species hummingbird guild seasonally inhabiting the Chiricahua Mountains of southeastern Arizona. *E. fulgens* will readily feed on nectar in artificial feeders, but use declines when feeders are defended by dominant Blue-throated Hummingbirds (*Lampornis clemenciae*) (Pimm et al. 1985, Powers and Conley 1994, Sandlin 2000a, Powers et al. 2003). This behavior is substantially different from that exhibited by

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Black-chinned Hummingbirds (*Archilochus alexandri*), another subordinate species, which consistently intrudes on *L. clemenciae* territories in attempts to gain a nectar reward (Powers and Conley 1994). There are few natural flowers available in many portions of the Chiricahua Mountains prior to onset of monsoon rains, and arthropods may be the only nearby alternative energy source for *E. fulgens* (Pimm et al. 1985). The idea that *E. fulgens* has the ability to subsist only on arthropods is not new. Marshall (1957:81) suggested that *E. fulgens* can inhabit pine-oak (*Pinus* spp.–*Quercus* spp.) woodlands because it "can dispense with moist habitat and flowers" and switch to arthropod consumption.

We conducted this study to ascertain if arthropods could be used as an alternative energy source when nectar availability is restricted and if the use of arthropods for energy is a feasible strategy that allows *E. fulgens* to reduce competitive interactions with territorial *L. clemenciae*. Evidence from behavioral, morphological, and physiological experiments are presented to demonstrate the energetic importance of arthropod foraging to hummingbirds.

METHODS

Study Animals.—Males of three species were used in this study: *E. fulgens* (~7.5 g), *L. clemenciae* (~8.0 g), and *A. alexandri* (~3.0 g). All three species occur in southeastern Arizona during summer and use different foraging strategies (Pimm et al. 1985, Powers and Conley 1994, Sandlin 2000a). *L. clemenciae* is a dominant species, defending territories along borders of riparian canyons. *A. alexandri* is non-territorial at our study site and robs nectar from territories defended by *L. clemenciae*. *E. fulgens* is also non-territorial, but appears to forage as a trapliner (Powers 1996), avoiding many competitive interactions at dense flower aggregations.

Study Area.—This study was conducted at the American Museum of Natural History's Southwestern Research Station in the Chiricahua Mountains, Cochise County, Arizona (31° 50′ N, 109° 15′ W; 1,700 m asl). Habitat at the station is largely riparian, bordered by oak woodland and a mixed deciduous/coniferous forest. Pimm et al. (1985) provide a more detailed description of the habitat. This forest endures a pronounced dry season from November until monsoon rains begin in early July that can dramatically affect the amount of nectar available (Li and Brown 1999).

Feeding Stations.—Twenty feeding stations in areas with vegetation that provided many potential perching sites were established for behavioral observations within the boundaries of the field station. This increased the probability that arthropod foraging could be observed in conjunction with nectar foraging. Each individual feeding station consisted of either a Perky-Pet Glass Feeder (Model No. 203-CP, Woodstream Corp., Denver, CO, USA) with the perch and corolla removed, or a triplet feeder constructed from three smaller Perky-Pet plastic singlet feeders (Model No. 214, Woodstream Corp., Denver, CO, USA) connected with Velcro® strips. The feeders were suspended from either a tree branch or a wire hook attached to a vertical length of PVC pipe. The height of the feeders (distance from the ground to the bottom of the feeder) ranged from 0.74 to 2.10 m. A 0.52 M (18% weight/weight) sucrose solution, a concentration typical of nectars in many hummingbird flowers (Baker 1975), was used at all the feeding stations.

Observations were made at four different time intervals for 97 hrs throughout the day during June and July 1998 and 1999. The timed intervals were: early morning (0500–0730 hrs MST), late morning (0800–1130 hrs), late afternoon (1500–1800 hrs), and early evening (1815–1930 hrs). The time of day each feeding station was visited was randomized to ensure an unbiased examination of both nectar and arthropod foraging over all times of day in all habitat types.

Arthropod Foraging.—The amount of time birds spent foraging for arthropods near the feeding stations was recorded. Arthropod foraging was divided into two modes: perch foraging and aerial foraging. Foliage gleaning or other known modes of arthropod foraging (Stiles 1995) were not detected. Perch foraging occurs when birds forage for arthropods while sitting on a perch (no flight is involved). This mode of arthropod foraging has been noted in a few hummingbird species (Pitelka 1942, Brice 1992). Typical behaviors include tongue extension, the bill opening, "gulping", or the head darting back and forth. Arthropod foraging data were only taken when it was clear that birds were attempting to catch arthropods (often the vantage point made it possible to see arthropod capture). Time spent perch foraging was measured by starting a stopwatch when a bird opened its bill, extended the tongue, or when the bird gulped (indicating the initiation of an arthropod foraging bout). The

number of attempts the bird made for arthropods was counted with the stopwatch running and the measurement was terminated when the bird flew, vocalized, scratched, rubbed its bill, preened its feathers, or lost active interest. The approximate height of the perch where the event occurred was recorded after recording the time and the number of attempts.

The second major mode of arthropod foraging, aerial flycatching, occurs during hovering or slow forward flight (Stiles 1995). We measured the duration of aerial flycatching bouts with a stopwatch from the time the bird left its perch until it returned to a perch or when the bout had clearly ended. The number of foraging attempts during a bout was estimated (we could not reliably count actual captures) by counting the number of head lunges (indicating a capture attempt). The height of the perch from which the bout was started was estimated visually.

Crop and Gizzard Analysis.—Crop and gizzard data came from samples taken by dissection of 17 birds ($n = 5$ *L. clemenciae*, $n = 6$ *E. fulgens*, and $n = 6$ *A. alexandri*) during June and July 1996. Gut contents were preserved in 95% ethanol. Whole or nearly whole arthropod specimens were identified to the lowest possible taxon. Measurements of the length of whole arthropods were made to calculate an approximate size range for arthropod prey. The crop and gizzard contents were dried to a constant mass in a drying oven (65° C) so we could compare the relative mass of arthropod contents for each hummingbird species.

Measurements were standardized to compare the amount of arthropod material in the gut between species by dividing the mass of arthropod material collected by bird metabolic body mass ($g^{0.75}$; the exponent approximately describes the relationship between body mass and metabolic rate; Calder and King 1974).

Gut Allometry.—The gut mass and length of each species were compared with 10 and eight other hummingbird species, respectively (M.-V. López-Calleja, C. Martínez del Rio, and J. E. Schöndube, unpubl. data). The intestines, from proventriculus to cloaca, were removed from birds killed by thoracic compression and immediately placed in 1.02% saline. The intestine was flushed with saline, blotted dry, and weighed to the nearest 0.01 g after any fat and mesentery were removed. Total length was measured to the nearest 0.1 mm with a digital caliper after the intestine was gently straightened. The relationship

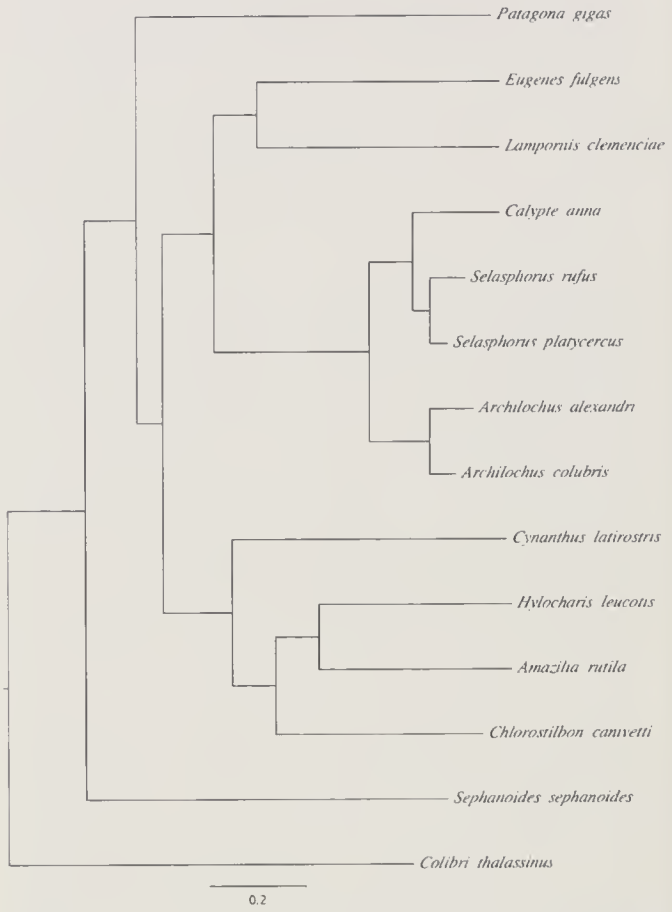

FIG. 1. Presumed phylogeny of 14 hummingbird species used in our phylogentic independent contrasts. A 0.2 branch-length scale is below the physlogenetic tree. The phylogeny is based on McGuire et al. (2007) with placement of *C. latirostris* based on García-Deras et al. (2008).

between gut length, gut mass, and body mass was examined using standard linear least-squares regression as well as phylogenctically independent contrasts (PIC; Felsenstein 1985, Garland et al. 1992). We performed least-squares regressions of log gut mass versus log body mass and log gut length versus log body mass for standard analysis. We calculated PIC for log body mass, log gut mass, and log gut length (Garland et al. 1992). The phylogeny and relative branch lengths used in our PIC analysis were based on McGuire et al. (2007) and Garcia-Deras et al. (2008) (Fig. 1). The maximum branch length was arbitrarily set at 1.0 with shorter branch lengths scaled appropriately. PIC analysis is robust to branch length variation (Garland et al. 1999) and setting branch lengths in this manner are unlikely to influence PIC results. Absolute values of standardized contrasts were correlated with their branch lengths, and branch lengths were increased by a factor of 10 and log transformed. This made correlations non-significant and contrasts were

weighted equally in subsequent analyses. Standardized contrasts were positivized according to Garland et al. (1992). We performed least-squares regression through the origin on positivized contrasts of log gut mass versus log body mass and log gut length versus log body mass.

Respiratory Quotient.—Respiratory quotient (RQ) measures the proportion of carbohydrate fuel an animal catabolizes during the measurement process by comparing carbon dioxide production with oxygen consumption ($RQ = Vco_2/Vo_2$). A measurement close to 1.0 represents pure carbohydrate use, while for birds an RQ close to 0.7 represents pure protein/fat use. Comparing RQs between species provides a view of the importance of nectar as a fuel at a given point in time. A bird foraging more on arthropods might be expected to have an RQ closer to 0.7. We predicted RQs for wild-caught *E. fulgens* would be lower than those for the other two species.

Birds were captured in mist nets three times each day (morning, midday, and late afternoon) and randomly assigned to one of two groups: (1) those caught from the wild and not fed, and (2) those birds that were fed sucrose solution after being caught but prior to RQ measurements. Fed birds were allowed to drink their fill of 0.86 M sucrose solution, and served as a control because they were presumably catabolizing primarily carbohydrate. The RQ of unfed individuals was expected to reflect the "normal" metabolic substrate for a bird at a certain time of day.

Measurements of O_2 consumption (Vo_2) and CO_2 production (Vco_2) were made using an open-circuit, positive-pressure respirometry system (Powers 1991). Body mass was measured to the nearest 0.1 g both before and after trials using a portable balance (Model No. LS 200, Ohaus Corp., Pine Brook, NJ, USA). The birds for each trial were kept for about 0.5 hr in a metabolism chamber within an environmental chamber at a constant temperature (27 °C) prior to making measurements. Metabolism chambers consisted of a large Mason jar (effective volume: 800 ml) for *E. fulgens* and *L. clemenciae* or a small Mason jar (effective volume: 380 ml) for *A. alexandri*. Metabolism chambers were placed in an environmental control chamber (I-35L, Percival Scientific, Perry, IA, USA). Temperatures were recorded to the nearest 0.1 °C using a Physitemp Bat-12 (Physitemp Instruments, Clifton, NJ, USA) and a Cu-Cn thermocouple. The flow rate of dry, CO_2-free air through the metabolism chamber was 500 ml/min. The inlet air passed through soda lime and Drierite to remove ambient CO_2 and water vapor, respectively, prior to passing through an O_2 analyzer (Model No. S-3A, Applied Electrochemistry, Naperville, IL, USA) and a CO_2 analyzer (Model No. LI-6262, LI-COR Biosciences, Lincoln, NE, USA). Data acquisition and analysis were with a Power Macintosh (Model No. 7200, Apple Computer Corp., Cupertino, CA, USA) using Warthog LabHelper and LabAnalyst software (Mark Chappell, University of California, Riverside, CA, USA).

Statistical Analysis.—We used nonparametric analysis of variance (Kuskal-Wallis test; Zar 1974) to evaluate differences among sample means. *Post hoc* testing was by multiple comparisons using Mann-Whitney *U*-tests (Zar 1974) when more than two groups were compared with alpha values adjusted using the Bonferroni correction. Curves illustrating allometric relationships were plotted using simple linear regression and the extent of variation explained by the regression is reported as r^2 (Zar 1974). All statistical calculations used SPSS 16.0.1 (SPSS 2007). Values reported are means ± SD.

RESULTS

Arthropod Foraging.—Individual *A. alexandri* were difficult to locate and observe foraging for arthropods, possibly because the presence of one or more aggressive *L. clemenciae* motivated these birds to remain inconspicuous. *E. fulgens* and *L. clemenciae* both exhibited a higher arthropod foraging rate aerially than while perched (*E. fulgens*: $U_{1,81} = 21.5$, $P < 0.001$; *L. clemenciae*: $U_{1,81} = 27.9$, $P < 0.001$; Fig. 2). *E. fulgens* had a higher aerial foraging rate than *L. clemenciae* ($U_{1,113} = 4.8$, $P = 0.03$). *L. clemenciae* perhaps compensated for the lower aerial foraging rate by spending more time in areal foraging than *E. fulgens* ($U_{1,25} = 6.93$, $P = 0.01$; $\bar{x} = 0.09 \pm 0.1$ min/hr for *E. fulgens*, $\bar{x} = 0.52 \pm 0.6$ min/hr for *L. clemenciae*). The majority of individual *E. fulgens* engaged in aerial arthropod foraging (87% of 93 observations) rather than perch foraging (13% of 93 observations). Individual *L. clemenciae*, in contrast, divided arthropod foraging activity more evenly with 45% engaged in perch foraging and 55% foraging aerially (95 total observations). These birds would typically drink from a feeder and then perch in close proximity to the feeder. *L. clemenciae* would often engage in

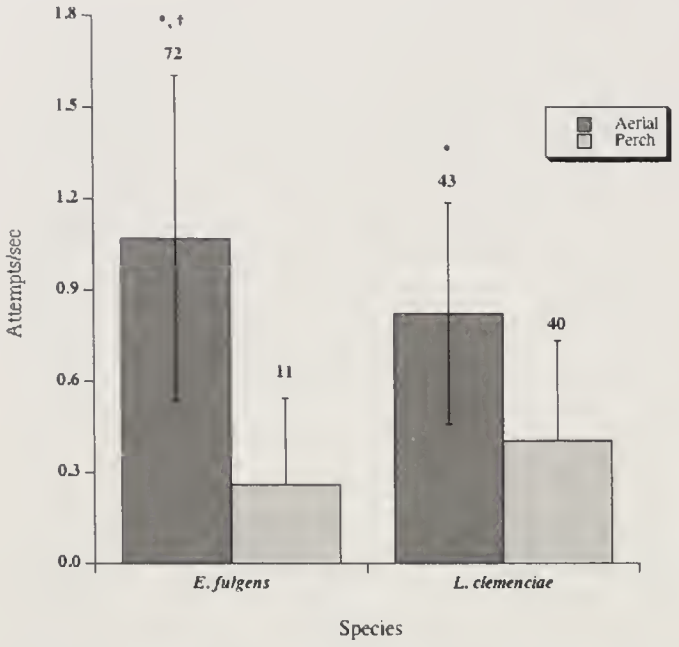

FIG. 2. Mean (± SD) number of insect capture attempts per second for *E. fulgens*, and *L. clemenciae* during a foraging bout. Numbers above the error bars are sample sizes. The "*" indicates a significant difference between the aerial and perch values for both *E. fulgens* and *L. clemenciae*. The "†" indicates a significant difference between aerial values for *E. fulgens* and *L. clemenciae*.

this behavior for a short time and then fly to defend the nearest feeder or to feed from it.

There was a marked difference in the average height from which the two species foraged for arthropods with *E. fulgens* perching at a greater height in both modes than *L. clemenciae* (aerial foraging height $U_{1,81} = 32.2$, $P < 0.001$; $\bar{x} = 9.9 \pm 4.7$ m for *E. fulgens*, $\bar{x} = 3.6 \pm 2.5$ m for *L. clemenciae*; perch foraging height: $U_{1,37} = 5.23$, $P = 0.02$; $\bar{x} = 5.9 \pm 4.0$ m for *E. fulgens*, $\bar{x} = 2.1 \pm 1.2$ m for *L. clemenciae*). Both species engaged in aerial foraging from a higher perch than when perch foraging (*E. fulgens*: $U_{1,59} = 5.39$, $P = 0.02$; *L. clemenciae*: $U_{1,59} = 5.84$, $P = 0.02$). *E. fulgens* appeared to remain high in the tree canopy (especially in *Juglans* spp. and *Platanus* spp.), while *L. clemenciae* perched in lower tree limbs or understory shrubs where it was closer to feeders.

Crop and Gizzard Contents.—Guts of *E. fulgens* contained the most arthropod taxa of our three study species (Table 1). The number of taxa represented (from 2 Classes and 4 Orders) is conservative because only arthropods that could be positively identified (to the lowest possible taxon) are reported. This meant identifying nearly whole specimens only. Absolute number of individuals in each of the taxa could not be calculated because most ingested arthropods were fragmented. All three identifiable members of the Order Hymenoptera were wasps. Several Homopteran specimens were the same type of leafhopper (Family Cicadellidae). There were three insects and one arachnid specimen that could not be further identified.

Numbers and size range of whole arthropods as well as the dry mass of all arthropod material collected from the three hummingbird species digestive tracts did not differ (dry mass: $H_{2,16} = 2.096$, $P = 0.351$; whole arthropods: $H_{2,16} = 2.228$, $P = 0.328$; Table 2).

Gut Allometry.—The linear regressions of gut mass and body mass, and the phylogentically independent contrasts (PIC) of gut mass and body

TABLE 1. Arthropod taxa found in crops and gizzards of hummingbird species in this study.

Species	A[a]	B[a]	C[a]	D[a]	E[a]	F[a]	G[a]	H[a]	I[a]
E. fulgens	X		X	X	X		X	X	X
L. clemenciae	X	X		X		X			
A. alexandri	X		X						X

[a] A = Class Insecta, Order Hymenoptera (length 3.4 – 5.8 mm); B = Class Insecta, Order Hymenoptera (length 2.5 mm); C = Class Insecta, Order Hymenoptera (length 1.0 mm); D = Class Insecta, Order Homoptera, Family Cicadellidae; E = Class Insecta, Order Diptera; F = Class Insecta (unknown Order[b]); G = Class Insecta (unknown Order[b]); H = Class Insecta (unknown Order[b]); I = Class Arachnida, Order Araneae.
[b] Different from other listed categories.

TABLE 2. Arthropods ($\bar{x} \pm$ SD) in crops and gizzards of hummingbirds in this study.

Species	*n*	Whole arthropods (#/individual)	Arthropod length (range, mm)	Dry mass ($mg/g^{0.75}$)
L. clemenciae	5	1.8 ± 3.0	2.47–2.55	0.9 ± 1.2
E. fulgens	6	6.2 ± 7.3	1.02–5.75	1.6 ± 1.6
A. alexandri	6	0.8 ± 1.1	0.97–3.50	1.6 ± 1.0

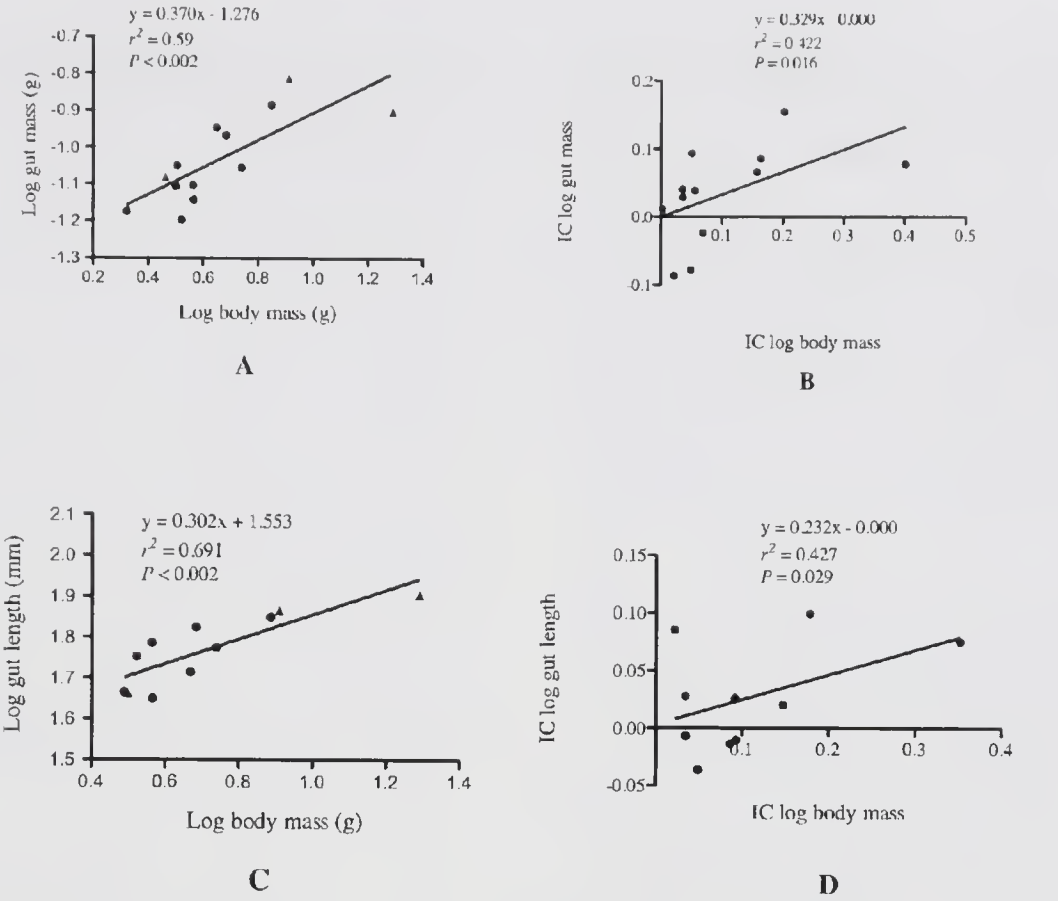

FIG. 3. The relationship between gut mass and length, and body mass in hummingbirds ranging in size from ~2 to 20 g. A and B are the standard linear regression and the linear regression of independent contrasts for gut mass as a function of body mass. C and D are the standard linear regression and the linear regression of independent contrasts for gut length as a function of body mass. Triangles in A and C are hummingbird species in this study.

mass were both significant (Fig. 3A, B) indicating body mass is a key factor affecting gut mass. The linear regression and PIC of gut length and body mass was also significant (Fig. 3C, D) indicating gut length varied with body mass.

Respiratory Quotient.—Respiratory quotient (RQ) within a species did not vary with time of day and the data for each species were pooled (Fig. 4). There was no difference between fed and unfed RQ for *A. alexandri* ($U_{1,16} = 2.91$, $P = 0.09$). There was a difference between fed and unfed RQ for both *E. fulgens* and *L. clemenciae* (*E. fulgens*: $U_{1,19} = 13.7$, $P < 0.001$; *L. clemenciae*: $U_{1,19} = 12.39$, $P < 0.001$). *E. fulgens* also had a lower unfed RQ than *A. alexandri* or *L. clemenciae* ($H_{2,39} = 6.88$, $P = 0.032$). There was little variation in unfed RQ in *E. fulgens*.

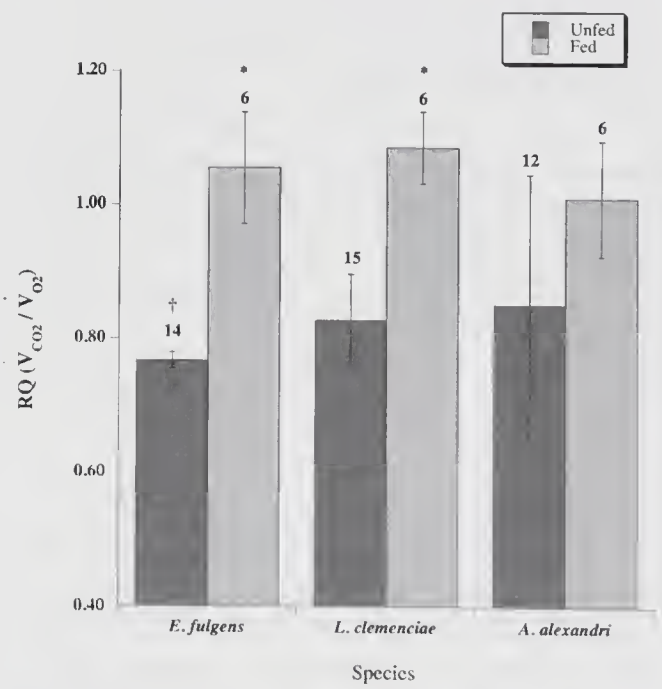

FIG. 4. Fed and unfed mean (± SD) respiratory quotient (RQ) for *A. alexandri*, *E. fulgens*, and *L. clemenciae*. The "*" indicates a significant difference between fed and unfed birds of the same species. The "†" indicates significance between unfed RQ for *E. fulgens* and the other species.

DISCUSSION

Nectar carbohydrates have been assumed to be the primary energy source for hummingbirds, but arthropods may also provide significant amounts of energy in addition to protein and lipids. Most insects from sweep net samples (Weathers and

Sullivan 1989) conducted in the Chiricahua Mountains were from the Orders Coleoptera, Homoptera, and Diptera. Weathers and Sullivan (1989) showed these insects have an average energy value of about 25 kJ/g (dry mass). Karasov's (1990) conservative estimate of the metabolizable energy of insets is 19.3 kJ/g (dry mass) compared to 16.4 kJ/g for nectar. Thus, energetically, arthropods have the potential to be more than a small supplement to a primarily carbohydrate diet. Hainsworth (1977) showed that if a hummingbird devotes equal time to nectarivory and flycatching, even low efficiency rates of ~40% can provide more energy than nectar feeding.

E. fulgens seemed to emphasize aerial foraging for arthropods. They spent the vast majority of their arthropod foraging time in this mode, had the highest frequency of capture attempts, and generally foraged from higher perches. *L. clemenciae* split their time more evenly between perch and aerial foraging, but actually spent more total time foraging for arthropods. It is possible that we actually observed a relatively small portion of their total arthropod-foraging activity because of the traplining behavior of *E. fulgens*.

Sandlin (2000a) suggested that *E. fulgens* switches to arthropod foraging to avoid the consequences of competition. Successful territorial species such as *L. clemenciae* maintain reliable nectar sources by defending them from invaders thereby gaining an energetic advantage (Powers et al. 2003). Thus, *L. clemenciae* may prefer to perch close to feeders, facilitating quick responses to intruders. This would be an efficient way to supplement their nectar diet for *L. clemenciae* foraging on arthropods while perched in a defensive position. Powers and Conley (1994) report that *L. clemenciae* are perched about 70% of the time, allowing them to both guard their territory and to forage for passing insects when available.

E. fulgens had the greatest diversity of arthropod species in its crop and gizzard (Table 2). These data corroborate the findings of Cottam and Knappen (1939) who examined gut contents of *E. fulgens* and *L. clemenciae* from the nearby Huachuca Mountains of Arizona. They found 13 different taxonomic specimens in the guts of *E. fulgens* but only seven in *L. clemenciae*. The reason for this difference is unclear. *E. fulgens* forages for arthropods higher in the canopy than *L. clemenciae* and the greater arthropod diversity in *E. fulgens* guts may reflect the diversity of arthropods available in the upper canopy. It is also possible the trapline-foraging behavior of *E. fulgens* diversifies the arthropod component of the diet (Colwell 1973, Feinsinger and Chaplin 1975). Our data show that *E. fulgens* and *L. clemencae* forage differently for arthropods but there is no evidence for a difference in arthropods consumed.

It is not possible to calculate the total contribution of arthropods to the diet of the hummingbirds in this study. It has been suggested the types of arthropods we found in the guts are digested quickly (Remsen et al. 1986, Stiles 1995). Thus, our measures of dry mass are probably a good index of short-term arthropod consumption and correspond reasonably well to the maximum rate arthropods were captured (range ~6 to 30 captures/hr assuming 100% capture efficiency and total arthropod digestion in 1 hr). The total digestible energy of arthropods consumed ranges from 0.2 to 0.4 kJ/day if arthropod dry mass is turned over in the gut hourly. Daily energy expenditure (DEE) is 82 kJ/day for *L. clemenciae* and 29 kJ/day for *A. alexandri* (Powers and Conley 1994). Our data suggest arthropods account for <1% of DEE assuming DEE for *E. fulgens* is similar to *L. clemencae*. These data suggest there is no difference in arthropod consumption or energy derived from arthropods for our three hummingbird species.

Our hummingbirds had gut masses and lengths that corresponded with their body size suggesting that none of the hummingbirds in this study has a unique gut design. Any ability to subsist on arthropods when nectar is scarce is likely a common trait in hummingbirds.

All three hummingbird species had RQ values <0.85 indicating they were not strictly catabolizing carbohydrate. The RQ of *E. fulgens* was statistically lower than the other two species but we are uncertain if the difference is truly enough to argue a difference in use of arthropods for energy. The low variability in *E. fulgens* RQ does at least hint at a difference in how the three species forage but the exact nature of this difference is unclear. The higher variability in the RQ of *L. clemenciae* and *A. alexandri* could correlate with time since their last nectar meal. The lower variability in *E. fulgens* could support more consistent arthropod consumption but it could also be explained by the routine capture of

traplining individuals that have not yet fed. RQ data alone are insufficient to draw conclusions regarding the importance of different metabolic substrates used by the hummingbirds in this study. Hummingbirds can rapidly switch between fatty acid and carbohydrate oxidation (Welch and Suarez 2007) making interpretation of a depression in RQ difficult.

E. fulgens differs behaviorally in arthropod foraging from at least *L. clemenciae* but there is no strong evidence that arthropod consumption provides a disproportionate amount of energy compared to the other hummingbird species in this study. It is probable that all three species energetically benefit from arthropods but quantifying the total contribution of insects to their energy budget is difficult. We still do not have a complete understanding of the role arthropods have in hummingbird nutrition but are hopeful that future studies using techniques such as stable isotope analysis might provide addition insight.

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ARMY ANT RAID ATTENDANCE AND BIVOUAC-CHECKING BEHAVIOR BY NEOTROPICAL MONTANE FOREST BIRDS

SEAN O'DONNELL,[1,3] ANJALI KUMAR,[1] AND CORINA LOGAN[2]

ABSTRACT.—We quantified resident and migrant bird attendance at army ant swarm raids (n = 48) in a neotropical montane forest. All observations were during seasons when Nearctic migrant birds are present. Bird species differed in army ant raid-attending behavior. Resident bird species attended 2 to 54% of raids, while migrants attended at lower maximum frequencies (2 to 21% of raids attended per species). Some resident and migrant bird species attended raids more frequently than expected based on capture rates in mist-net studies and point-count density surveys. Army ant raid attendance may be a regular element of foraging behavior for some resident species, and important in the wintering ecology of some Nearctic migrant species. The bird species that attended raids most frequently were predicted to show behavioral specializations for exploiting army ant swarms. Eight resident bird species (but no migrants) performed a specialized behavior, bivouac checking, by which birds sample army ant activity. Resident bird species' frequencies of raid attendance were positively associated with frequency of checking bivouacs (r = 0.68). We hypothesize the absence of obligate army ant-following birds in montane forests has favored performance of specialized behaviors for exploiting army ant raids by some resident birds. *Received 3 October 2009. Accepted 9 March 2010.*

Neotropical army ants (Formicidae: Ecitoninae) are top predators, and a diverse array of animal species associate with army ant colonies (Franks 1982, Franks and Bossert 1983, Brady 2003, Koh et al. 2004). Birds attend army ant foraging-raids to feed on arthropods and small vertebrates that flee from the advancing ants. Birds primarily attend the swarm raids of *Eciton burchellii* and *Labidus praedator* (Willis and Oniki 1978, Wrege et al. 2005). Bird flocks at army ant raids often include multiple species, and their composition is largely distinct from sympatric mixed foraging flocks of insectivores (Willis 1972, Willis and Oniki 1978, Otis et al. 1986, Willson 2004, Peters et al. 2008).

Some bird species are obligate army ant raid attendants that obtain most or all of their food at army ant swarms (Willis and Oniki 1978, Swartz 2001, Willson 2004, Brumfield et al. 2007). Other bird species attend raids opportunistically (Swartz 2001, Chaves-Campos 2003). Opportunistic army ant raid-attending bird species vary in their reliance on army ants (Willis 1972, Willis and Oniki 1978). Obligate army ant-following birds are agonistic toward other birds at raids in lowland forests. This interference competition reduces the value of ant raids as a food source to other birds (Willis 1966, Willis and Oniki 1978, Brumfield et al. 2007).

Obligate army ant-following birds are poorly represented or absent from montane forests (Willis and Oniki 1978, Brumfield et al. 2007). There are no obligate army ant-following birds at our study site near Monteverde, Costa Rica (Kumar and O'Donnell 2007). Birds from a diverse array of families attend army ant raids in the Monteverde area, including some resident and Nearctic migrant species (henceforth migrants; Vallely 2001, Kumar and O'Donnell 2007). We hypothesized that some montane bird species would exhibit behavioral specializations for exploiting army ant raids in the absence of local competition from obligate army ant-following birds. We asked whether some montane bird species attend raids more often than expected as a first test of this hypothesis. The frequency of raid attendance varies among Monteverde area birds, but attendance frequency alone does not account for possible effects of local abundance (Vallely 2001, Kumar and O'Donnell 2007, Peters et al. 2008). We extended our previous analyses estimating the effects of species' relative abundance on army ant raid attendance in this study. Bird abundance estimates were derived from previously published mist-net captures and point-count densities (Young et al. 1998, Jankowski et al. 2009).

We predicted the most frequent raid attendant birds would be more likely to exhibit specialized behaviors for exploiting army ant swarms (Willis 1972, Willis and Oniki 1978, Swartz 2001, Chaves-Campos 2003). We ascertained whether

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montane forest birds perform bivouac-checking behavior to test this prediction. Bivouac-checking birds visit *Eciton burchellii* temporary nests (bivouacs) as the ant foraging raids start in the morning, and again in the evening. Bivouac-checking birds may assess army ant raid activity and direction in the morning, or whether ants are emigrating to a new bivouac site in the evening (Swartz 2001, Chaves-Campos 2003). We correlated bird species' frequencies of bivouac checking with their frequencies of attendance at army ant raids to examine whether raid attendance frequency and bivouac-checking behavior were associated among bird species.

METHODS

Study Site.—Our sample sites spanned the continental divide in the Tilarán Mountain Range near Monteverde, Puntarenas Province, Costa Rica (10° 18′ N, 84° 47′ W). The Monteverde area includes forest reserves with adjacent privately held continuous forest and associated forest fragments (Guindon 1997, Haber 2000, Harvey 2000, Jankowski et al. 2009). We collected data in forests between 1,175 m above mean sea level (m asl) and 1,580 m asl elevation on the Pacific Slope, and between 985 and 1,680 m asl elevation on the Atlantic Slope. Our raid attendance samples included four life zones (Holdridge life zone system; Holdridge 1966, Guindon 1997, Young et al. 1998, Young and MacDonald 2000).

Sampling Bird Flock Composition.—We collected data during seasons when migrants occur in the Monteverde area (Stiles and Skutch 1989, Garrigues and Dean 2007). The four field trips collectively spanned much of the period of migrant presence (mid-Sep to late May): 11 January–4 March 2005 (dry season), 5 October–11 December 2005 (late wet season/onset of dry season), 19 December 2007–1 January 2008 (early dry season), and 7–10 April 2008 (late dry season). We observed birds at 48 army ant raids during these trips. The army ant raids involved three swarm-raiding army ant species (*Eciton burchellii*, $n = 40$; *Labidus praedator*, $n = 5$; and *L. spinninodis*, $n = 3$). We did not separate army ant species in our analyses as the *Labidus* species raids were distributed across all life zones, and army ant species had no measurable effect on attending bird flock composition in the Monteverde area (Kumar and O'Donnell 2007). We observed a maximum of one swarm per day and alternated sampling dates among elevations to minimize order effects. We treated each army ant swarm as an independent data point because observations were separated in space and time. Observations were made during the diurnal active raid period of surface-foraging army ants. Start times ranged from 0900 to 1600 hrs local time (CST).

We located flocks of army ant swarm-attending birds or foraging army ant columns by searching along established trails. We walked to swarm raid fronts where birds fed and positioned ourselves at the best location for unobstructed viewing of the swarm front; this was usually off to one side and facing in the direction the swarm was moving. If the raid or the bulk of bird activity shifted location during observations we walked to a new observation spot while attempting to avoid disturbing the birds. We noted all bird species and the number of individuals that were present upon our arrival (Coates-Estrada and Estrada 1989). The observation sessions lasted for 1 hr except when raid activity ceased, heavy rainfall began, or ants traversed impassable terrain ($\bar{x} \pm$ SD observation time = 47 ± 18 min). We analyzed only those flocks for which all attending birds were identified to species.

We collected four types of data on bird flock composition and bird behavior at the army ant swarms. (1) Start and end time to the nearest min. (2) Latitude/longitude coordinates and elevation to the nearest 10 m asl were taken with a handheld Geographic Positioning System (GPS) unit or an air pressure altimeter. Elevations were confirmed from topographic maps. (3) We identified all birds seen in attendance to species based on plumage appearance, behavior, relative body size, geographic range, and vocalizations (Stiles and Skutch 1989, Garrigues and Dean 2007). A bird had to be observed collecting prey that was fleeing from ants to be counted as an attendant. Birds were categorized as residents or migrants. (4) We recorded the number of individuals of each bird species present. The birds were not banded and we could not distinguish individuals that left the raid and returned from newly arriving swarm attendants. Thus, we used the maximum number of individuals that were observed simultaneously as a conservative estimate of the number of attending birds from each species (Coates-Estrada and Estrada 1989).

Bivouac-checking Observations.—We conducted 15 systematic watches for bivouac-checking behavior at *E. burchellii* bivouacs following

Swartz (2001). We sat on the ground or on folding chairs at sites 5 to 10 m from the bivouac, facing the entrance of the bivouac shelter. We chose locations that were partially concealed by vegetation but had an unobstructed view of the bivouac entrance. Our observation durations ranged from 60 to 120 min ($\bar{x}$ = 87.4 min/session; 21.9 hrs of observation). Like Swartz (2001), we conducted 12 observation sessions in the morning (start times 0440 to 0800 hrs) and extended the protocol by conducting three bivouac watches in the afternoon (start times 1533 to 1630 hrs). We recorded bivouac-checking behavior and counted a bird as checking the bivouac if it first flew toward the bivouac site and perched within 5 m of the bivouac. The bird then had to either peer at the bivouac shelter entrance, or land among the ants when ants were active outside the bivouac to be counted. We noted bird arrival time to the nearest minute and, whenever possible, recorded the duration of each bird's visit. We also recorded the species identity of birds that were observed performing bivouac-checking behavior while we were collecting other data (n = 5 observations; Swartz 2001). We used the same behavioral criteria for bivouac checking as during systematic observations. Dates of bivouac-checking observations were: 15 November to 3 December 2005, 22 to 29 December 2007, 7 to 10 April 2008, and 5 to 25 July 2009. We made six systematic and two opportunistic bivouac-checking observations during seasons when Nearctic migrants are present at the field site.

We could not identify birds as individuals as birds were not banded and many species were sexually monomorphic in plumage. We used only one visit/species/observation session to estimate frequencies of bivouac checking. All but one of our bivouac-checking observations were in the premontane wet forest life zone. We sampled bivouac checking at elevations from 1,100 to 1,430 m asl; one systematic observation was conducted at a higher elevation (1,575 m asl) in the lower montane wet forest life zone, but no birds were recorded bivouac checking at this site. We also noted if birds vocalized while bivouac checking in 2008 and 2009. We used observations of bird attendance at a larger sample of army ant raids (n = 54) for comparisons of raid attendance with bivouac checking. These data were collected during several field trips between 25 January 2005 and 10 April 2008. These raids partially overlap with the migrant season raid sample, but all were observed in the same life zone and over a similar range of elevations as our bivouac-checking observations (1,100 to 1,475 m asl).

Statistical Analyses.—We calculated two measures of bird species attendance at swarm raids based on species richness and individual abundance at the 48 migrant season raids (Coates-Estrada and Estrada 1989): (1) the percent of raids at which each species was present, and (2) the percent of all raid-attending birds accounted for by each species. We used two independently collected data sets to estimate forest understory activity and relative abundance of bird species. We compared these with our abundance measure of army ant raid attendance (i.e., each species' percent of all birds at raids) to identify species that were present at raids more often than expected by chance. The estimate of relative activity came from mist-net data from Monteverde area forests (Young et al. 1998). We calculated the number of mist-net captures for each attending bird species from Young et al. (1998: table 2), summing total captures for each species over the four life zones that overlapped our sample area. Mist-net studies of bird abundance must be interpreted with caution (Remsen and Good 1996). For example, bird species may differ in probability of being caught in nets in the understory. We used an independently-derived estimate of relative abundance from standardized auditory and visual point-count data to complement the mist-net data. The point-count data also came from sites largely overlapping with our observations (Jankowski et al. 2009: supplementary table 1).

We followed Peters et al. (2008) to calculate two indices of raid attendance for each bird species. We regressed each species' proportion of the total birds observed at raids against its total captures in the mist-net studies (Young et al. 1998), and against its total/ha abundance estimated from point counts (Jankowski et al. 2009). We calculated residuals from these two linear regressions and used the residuals as indices of raid attendance. We identified species as high-frequency army ant raid attendants when their index value (regression residual) was higher than the upper 95% confidence interval (CI) value from the corresponding linear regression model. We calculated the mist-net index separately for residents and migrants because resident birds were mist-netted year-round, including months when migrants are absent. We could not calculate

a point-count index for migrants as they were not recorded in the point-count study, in part because migrants rarely vocalize outside their breeding ranges (Jankowski et al. 2009).

We asked whether bird species differences in raid attendance were correlated with bivouac-checking frequency. We calculated the Pearson correlation between an index of raid attendance frequency (i.e., the point-count attendance index) and bivouac-checking frequency for the 31 resident bird species observed at army ant raids in the bivouac-checking sample elevation range.

RESULTS

Bird Flock Composition at Ant Raids.—We observed 54 species of birds attending raids during the period of migrant presence (Table 1). The number of bird species in flocks at army ant raids ranged from one to 17 ($\bar{x} \pm SD = 4.73 \pm 3.27$), while the number of migrant species ranged from zero to six (0.79 ± 1.29). We recorded 11 species of migrants attending raids; two were thrushes (Turdidae), one was a vireo (Vireonidae), and eight were wood warblers (Parulidae) (Table 1). We recorded 13 bird species at raids that had not been noted as army ant raid attendants in the Monteverde area previously (11 new residents and 2 new migrants). Migrants participated in 21 (43.8%) of the flocks at army ant swarms. None of the swarm-attending flocks was comprised only of migrants.

Resident Species Differences in Raid Attendance.—Resident bird species varied widely in frequency of raid attendance. Resident species ranged from 2.1 to 54.2% of army ant raids attended, and from 0.2 to 10.8% of the individual birds at army ant raids (Table 1). Species' point-count densities and mist-net captures were positively but weakly correlated ($r = 0.42$, $n = 54$, $P < 0.01$). These measures provide different information on bird species' baseline rates of occurrence in the habitat. Both measures of baseline density were non-significantly related to army ant raid attendance by the 43 resident bird species. Point-count estimates of bird species' abundances were poor predictors of species occurrence at army ant raids ($R^2 = 0.004$, df = 53, $P = 0.64$). Similarly, capture frequency in mist-net studies was weakly associated with attendance at army ant raids ($R^2 = 0.06$, df = 42, $P = 0.10$). Both indices of frequency of raid attendance indicated strong species differences in frequency of army ant raid attendance after accounting for density effects. There was high consistency between the two indices of which bird species attended army ant raids at higher than expected frequencies. Seven resident bird species' frequencies at raids exceeded the 95% CI value predicted by linear regression of raid attendance on mist-net capture frequency (Fig. 1). Six of these seven species (and one other) were significantly more frequent at raids than expected based on point-count densities (Fig. 1).

Migrant Species Differences in Raid Attendance.—Relative abundances of migrants at raids spanned an order of magnitude among species in terms of percent of raids attended (2.1 to 20.8%) and in percent of individual birds seen at raids (0.19 to 1.87%; Table 1). The Kentucky Warbler (*Oporonis formosus*) was the most frequent migrant at army ant raids by both measures. Mist-net capture frequency of migrant species was a poor predictor of their proportion of raid-attending birds ($R^2 = 0.07$, $n = 11$, $P = 0.43$). Examination of residuals from this analysis suggests three migrant bird species attended raids more frequently than expected by mist-net captures (Fig. 2).

Bird Species that Check Bivouacs.—We observed eight species of birds from eight families checking bivouacs in the Monteverde area (Table 1). Birds checked bivouacs during 10 of the 15 systematic watches (67%); birds were seen bivouac checking during 67% of both morning and afternoon watches. The number of species seen during an observation session ranged from zero to four ($\bar{x} = 1.47$ species). We did not see more than one individual of a given species arrive at the same time. Birds of three species were present at a bivouac simultaneously on one occasion, but were not seen interacting. Six species checked bivouacs both in the morning and afternoon (Table 1); the other two species checked in the morning but were seen only once.

Bird Behavior During Bivouac Checks.—We obtained duration data for 17 bivouac checks by six bird species (the bird was not identified on one timed visit). Bivouac-check durations pooled across species varied from a few seconds to several minutes (range = 5 to 360 sec; $\bar{x} \pm SD = 103 \pm 126$ sec). Visit lengths did not differ significantly among species (Kruskal-Wallis test, $X^2 = 7.6$, df = 5, $P = 0.18$).

Three species, Orange-billed Nightingale-Thrush (*Catharus aurantiirostris*), Rufous-and-white Wren (*Thryothorus rufalbus*), and Rufous-

TABLE 1. Frequencies of occurrence of birds as foragers at army ant swarm raids in montane forests near Monteverde, Costa Rica. Nearctic migrants are indicated by an asterisk *. Species not seen in previous studies of avian army ant raid attendance in the Monteverde area are indicated by a plus symbol +.

Species	Number of raids attended (n = 48)	% of raids attended	Number of birds (n = 316)	% of birds
Orange-billed Nightingale-Thrush *Catharus aurantiirostris*	26	54.2	58	10.8
White-eared Ground Sparrow *Melozone leucotis*	18	37.5	29	5.4
Blue-crowned Motmot *Momotus momota*	15	31.3	21	3.9
Brown Jay *Cyanocorax morio*	14	29.2	37	6.9
Slaty-backed Nightingale-Thrush *Catharus fuscater*	10	20.8	21	3.9
Rufous-and-white Wren *Thryothorus rufalbus*	10	20.8	13	2.4
Rufous-capped Warbler *Basileuterus rufifrons*	10	20.8	11	2.1
Kentucky Warbler **Oporornis formosus*	10	20.8	10	1.9
Immaculate Antbird *Myrmeciza immaculata*	9	18.8	22	4.1
Wood Thrush **Hylocichla mustelina*	7	14.6	7	1.3
Golden-crowned Warbler *Basileuterus culicivorus*	6	12.5	8	1.5
Slate-throated Whitestart *Myioborus miniatus*	6	12.5	7	1.3
Yellowish Flycatcher *Empidonax flavescens*	6	12.5	6	1.1
Three-striped Warbler *Basileuterus tristriatus*	5	10.4	12	2.2
Ruddy Woodcreeper *Dendrocincla homochroa*	5	10.4	7	1.3
Wilson's Warbler **Wilsonia pusilla*	5	10.4	7	1.3
Swainson's Thrush **Catharus ustulatus*	5	10.4	5	0.9
Blue-throated Toucanet *Aulacorhynchus prasinus*	4	8.3	6	1.1
Chestnut-capped Brush Finch *Arremon brunneinucha*	4	8.3	4	0.8
Ruddy-capped Nightingale-Thrush *Catharus frantzii*	4	8.3	4	0.8
White-throated Thrush *Turdus assimilis*	3	6.3	8	1.5
Azure-hooded Jay *Cyanolyca cucullata*	3	6.3	5	0.9
10 species including one migrant: Black-and-white Warbler **Mniotilta varia*	2	4.2	2 or 3	0.4 or 0.6
22 species including 6 migrants*: Chestnut-sided Warbler, *+Dendroica pensylvanica*; Black-throated Green Warbler, *D. virens*, Ovenbird, *+Seiurus aurocapilla*; Golden-winged Warbler, *+Vermivora chrysoptera*; Canada Warbler *Wilsonia canadensis*; Philadelphia Vireo, *Vireo philadelphicus*	1	2.1	1 or 2	0.2 or 0.4

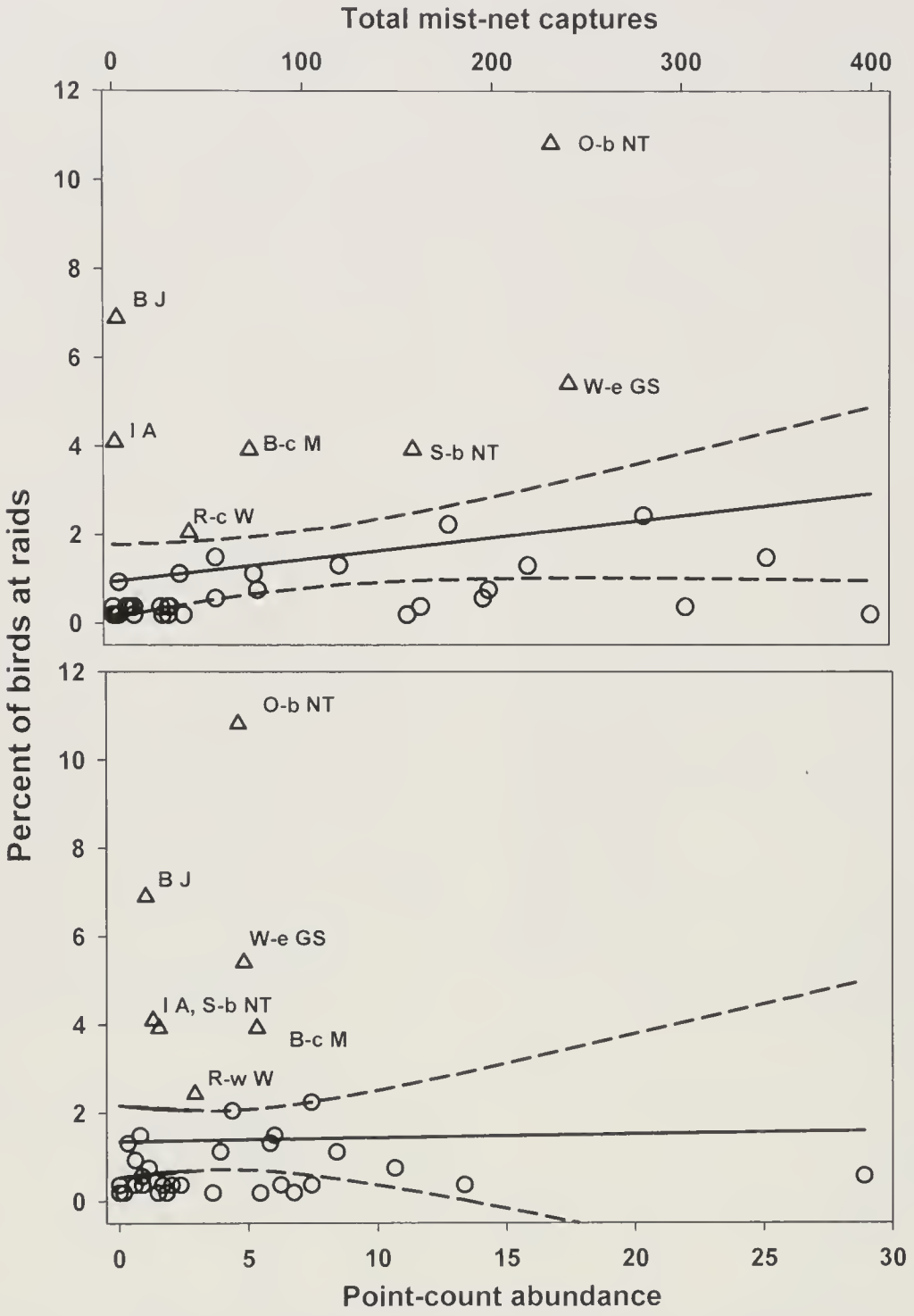

FIG. 1. Frequency of army ant raid attendance plotted against estimated local abundance for montane resident bird species (Monteverde, Costa Rica). Solid line: linear regression best fit. Curved dashed lines: 95% confidence intervals (CI). Triangle symbols indicate species with raid attendance above the 95% CI (O-b NT = Orange-billed Nightingale-Thrush; B J = Brown Jay; W-e GS = White-eared Ground Sparrow; IA = Immaculate Antbird; B-c M = Blue-crowned Motmot; S-b NT = Slaty-backed Nightingale-Thrush; R-c W = Rufous-crowned Warbler; R-w W = Rufous-and-white Wren).

capped Warbler (*Basileuterus rufifrons*), either sang or called while bivouac checking. Ruddy Woodcreepers (*Dendrocincla homochroa*) and/or Orange-billed Nightingale-Thrushes called or sang in the vicinity of bivouac sites during eight observation sessions, even when birds were not observed checking the bivouac. Individuals of these species apparently circled the bivouac site at distances of 10 to 15 m, calling or singing from different perches.

Raid Attendance and Bivouac Checking.—Bivouac checking was associated with high frequencies of army ant raid attendance. We observed 42 species of birds attending 54 army ant raids in the elevation range where we sampled bivouac checking. All bird species that checked bivouacs

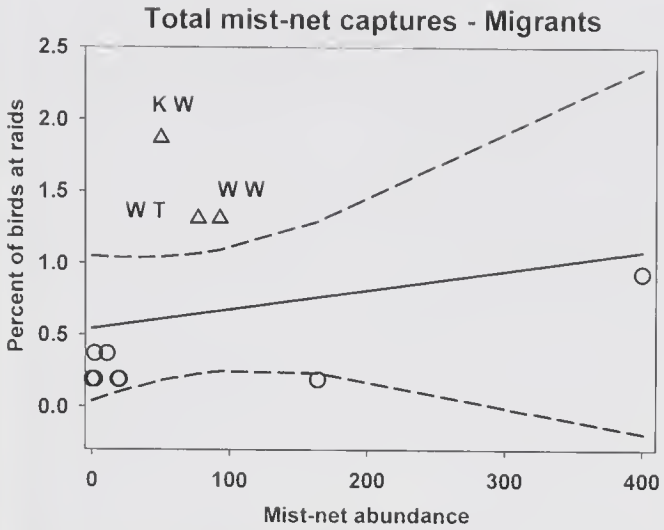

FIG. 2. Frequency of army ant raid attendance plotted against estimated local abundance for migrant bird species (Monteverde, Costa Rica). Solid line: linear regression best fit. Curved dashed lines: 95% confidence intervals (CI). Triangle symbols indicate species with raid attendance above the 95% CI (KW = Kentucky Warbler; WW = Wilson's Warbler; WT = Wood Thrush).

were also seen attending ant raids. The eight species observed checking bivouacs were among the most frequent raid attendants (Table 2). Bivouac-checking birds represented 19.0% of the bird species at these raids, but 57.7% of individual birds at the raids. Furthermore, the percent of bivouacs checked by a species correlated positively ($r = 0.68$, $n = 31$, $P < 0.01$) with the point-count raid attendance index for the 31 resident bird species that attended raids in the same elevation range (Table 2).

Six of our systematic watches and two opportunistic observations were in months when Nearctic migrant birds are wintering in the Monteverde area (Nov, Dec, and Apr.). No migrant birds were seen checking bivouacs (Table 2).

DISCUSSION

Resident Bird Species Differences in Raid Attendance.—Frequency of mist-net capture and point-count densities did not predict variation in raid attendance among bird species observed. Bird species density was not an important determinant of frequency of army ant raid attendance, and bird species must vary in their frequency of raid attendance for other reasons. The two independently-derived indices of raid attendance for residents identified similar lists of bird species that were at raids more frequently than expected (Peters et al. 2008). These species may depend more heavily on army ants for food, and they may exhibit specialized behaviors for exploiting army ant swarms. These behaviors could include mechanisms for locating and orienting to the ants or to other attending birds, or abilities to track army ant colony activity and movements such as bivouac checking (Willis and Oniki 1978, Swartz 2001, Chaves-Campos 2003).

TABLE 2. Bird species observed attending army ant raids and checking bivouacs in montane forests near Monteverde, Costa Rica.

Common name	Scientific name (Family)	Percent of bivouac check observations ($n = 20$)	Afternoon bivouac-checking observed?	Percent of raids attended ($n = 54$)	Percent of birds at raids ($n = 327$)	Raid attendance index rank ($n = 31$ species)
Orange-billed Nightingale-Thrush	*Catharus aurantiirostris* (Turdidae)	50	Yes	59.3	20.2	1
Ruddy Woodcreeper	*Dendrocincla homochroa* (Furnariidae)	30	Yes	5.6	0.9	14
Rufous-capped Warbler	*Basileuterus rufifrons* (Parulidae)	15	Yes	35.2	7.6	5
Rufous-and-white Wren	*Thryothorus rufalbus* (Troglodytidae)	15	Yes	24.1	5.5	6
Blue-crowned Motmot	*Momotus momota* (Momotidae)	10	Yes	38.9	8.9	4
Blue-throated Toucanet	*Aulacorhynchus prasinus* (Ramphastidae)	10	Yes	9.3	2.4	8
White-eared Ground Sparrow	*Melozone leucotis* (Emberizidae)	5	No	48.1	11.9	2
Chirqui Quail-Dove	*Geotrygon chiriquensis* (Columbidae)	5	No	1.9	0.3	26

Ecological Implications of Bivouac-checking Behavior.—Only obligate army ant-following birds checked bivouacs in lowland neotropical forests, even at sites with opportunistic species that frequently attended raids (Swartz 2001, Chaves-Campos 2003). Swartz (2001) suggested bivouac-checking behavior can be used to distinguish obligate army ant-following bird species from opportunistic raid attendants. Performance of this specialized behavior by Monteverde resident birds indicates army ant swarms are an important food resource to some montane bird species. The relative importance of foraging at ant raids to bird diets has not been quantified, but species differences in raid attendance combined with bivouac-checking behavior indicate some specialization for foraging at army ant swarms. Two bird species were seen checking bivouacs only once, indicating that more montane birds would be seen performing this behavior with additional observations. Whether resident and migrant montane birds exhibit other specialized behaviors to enhance attendance at ant raids requires further study. Some resident attendants vocalized while checking bivouacs, including nightingale-thrushes (*Catharus* spp.). Calling and singing at bivouac sites by some residents may recruit other birds to attend raids (Chaves-Campos 2003).

Bivouac-checking birds devote time and energy to sampling army ant behavior without an immediate food reward, and possibly expose themselves to predators. Bivouac-checking bouts were generally short in duration, consistent with this behavior incurring some cost (Swartz 2001). Some bird species check bivouacs in the morning (at the start of raiding) and in late afternoon (when most colony emigrations begin: O'Donnell et al. 2009), suggesting that birds track movements of ant colonies as well as their daily raiding activity. Individually marking and tracking birds will be necessary to identify how many bivouacs the montane resident birds check on a given day, and how far they travel among bivouacs (Willson 2004, Chaves 2008).

We hypothesize that reduced (or absent) competition with obligate army ant-following birds in some montane forests removes biotic constraints on specialized raid-attending behavior for other species. Reasons for obligate army ant-following bird absence in the Monteverde area Pacific Slope are not known, but lack of local competition with obligate army ant-following birds may enhance the value of army ant swarms to opportunistic raid-attending birds. It remains to be tested whether these behaviors represent local evolutionary adaptations or plastic expression of behavior based on learning or cultural transmission. We predict that observations at other sites without obligate army ant-following birds will reveal specialized army ant raid-attending behaviors in additional bird species.

Ecological Implications of Migrant Raid Attendance.—Three species of migrants attended army ant raids more often than expected according to the mist-net capture-based index. The Kentucky Warbler and two thrushes (Wood Thrush [*Hylocichla mustelina*] and Swainson's Thrush, [*Catharus ustulatus*]) have been recorded as army ant-raid attendants from Mexico to Colombia (Willis 1966, 1984; Greene et al. 1984; Coates-Estrada and Estrada 1989; Roberts et al. 2000; Meisel 2004), as have several other migrants we observed attending army ant swarms (Willis 1966, Hardy 1974, Greene et al. 1984, Roberts et al. 2000, Meisel 2004, Rios et al. 2008). Army ant raid attendance is apparently consistent across the wintering ranges of some migrant birds. Swarm-raiding army ants do not occur in the breeding ranges of the migrants we recorded as raid attendants (Watkins 1985). Attendance at army ant raids by wintering migrants is a striking example of plasticity in foraging behavior, and of differences in foraging ecology between breeding and wintering habitats. Changes in foraging ecology are an important component of niche-switching between breeding and wintering sites (Nakazawa et al. 2004). Studies at South American sites are needed to learn if similar changes in foraging ecology, including army ant raid attendance, are exhibited by Austral migrant birds (Jahn et al. 2004).

Migrants were not at raids without residents. Residents may initiate raid-attending flocks that are later joined by migrants, possibly in part because residents are locally more abundant (Young et al. 1998, Jankowski et al. 2009). Some resident birds may also be more effective at locating or tracking army ant raids, in part due to specialized behaviors like bivouac checking. Migrants did not check bivouacs but could use other behavioral mechanisms for exploiting ant raids. Data on young migrant bird interactions with army ants during their first migration into the geographic range of these ants could reveal important developmental patterns, including roles

of learning and social transmission in the performance of raid-attending behavior.

All of the migrants we observed at raids are known to forage on other resources while wintering (Willis 1966, 1984; Di Giacomo and Di Giacomo 2006; SO'D and AK, pers. obs.). However, even occasional reliance on army ant swarm-raids as a food source may have implications for migrant bird conservation. The extent of reliance of migrants on army ants as a food source may affect fitness of birds and winter survival by migrants based on changes in army ant density. Army ant-foraging behavior and population dynamics are strongly affected by forest clearing and forest fragmentation (Franks 1982, Meisel 2006, Kumar and O'Donnell 2009). Habitat change effects on wintering migrants could be exacerbated through changes in army ant communities (Koh et al. 2004).

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MAROON-FRONTED PARROT (*RHYNCHOPSITTA TERRISI*) BREEDING HOME RANGE AND HABITAT SELECTION IN THE NORTHERN SIERRA MADRE ORIENTAL, MEXICO

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ABSTRACT.—The Maroon-fronted Parrot (*Rhynchopsitta terrisi*) is a threatened species endemic to pine-oak (*Pinus* spp.-*Quercus* spp.) forests in "sky islands" of the Sierra Madre Oriental in Mexico. We measured parrot (n = 10) home ranges during the breeding season (1999–2001) using radiotelemetry. Home ranges varied among years: 1999 = 12,379.05 ha, 2000 = 8,633.82 ha, and 2001 = 4,736.75 ha. Differences in home range size may reflect variation in distribution, abundance, and patchiness of food. Daily movements in 1999 were estimated as 23.6 km versus 13.7 km in 2000 and 26.8 km in 2001. Habitat preferences within the *Pinus* forest varied among nesting seasons. Preference in 1999 was for *Pinus-Abies-Pseudotsuga* forest and in 2000 and 2001 it was for *Pinus* forest and chaparral. This variation may be influenced by nesting behavior. Rapid landscape changes may necessitate planting and conserving pine forest to regenerate areas for long term conservation of Maroon-fronted Parrots. *Received 3 January 2008. Accepted 26 January 2010.*

Maroon-fronted Parrots (*Rhynchopsitta terrisi*) occupy temperate coniferous and mixed coniferous-deciduous forests of the Sierra Madre Oriental, Mexico, ranging from Nuevo Leon and Coahuila in the north to Queretaro in the south. Breeding occurs in a small area in Nuevo Leon and Coahuila where parrots nest in cavities and crevices in limestone cliffs that are often several hundred meters high. Maroon-fronted Parrots nest in aggregations and known nesting colonies have a long history of use. Nesting occurs in summer and early fall. Once breeding and nesting season ends, usually in November, parrots migrate south in the Sierra Madre Oriental (Enkerlin-Hoeflich et al. 1999). Recent counts suggest a total population of ~3,500 individuals (Valdes-Peña et al. 2008). These parrots are endemic and protected under Mexican Government regulations, as well as internationally (SEMARNAP 2000, Birdlife International 2007, CITES 2007).

Maroon-fronted Parrots feed mainly on pine (*Pinus* spp.) seeds (especially those of *Pinus strobiformis*, *P. montezumae*, *P. greggii*, *P. cembroides*, and *P. culminicola*), and flowers and fruits of agave (*Agave gentryi*) during the breeding season. They may fly long distances searching for food, and annual movement patterns vary considerably because of temporally and spatially erratic nature of pine cone crops (Enkerlin-Hoeflich et al. 1999). These parrots eat acorns of several oak species (SGOM, pers. obs.) during winter. Most pine forests in the region are relicts and regeneration is scant or absent once forests are destroyed by natural causes or cut for use by humans.

Radiotelemetry has been used as a tool in estimating parrot home range size because monitoring movements of neotropical parrots is difficult as they usually fly long distances, which allows opportunities to select among different forest habitats (Gilardi and Munn 1998). Our objectives were to use radiotelemetry to: (1) measure home range size, and (2) identify habitats used by breeding Maroon-fronted Parrots during three breeding seasons. We also estimated areal requirements for different habitats during breeding to effectively conserve and manage Sierra Madre Oriental forests and habitats for this important species.

METHODS

Our study was conducted in the northern Sierra Madre Oriental from 100° 16′ W, 25° 42′ N to 99° 50′ W, 24° 50′ N. This mountain chain is 600 km north-south and 80 km east-west. Elevation varies from 2,000 to 2,500 m above sea level with several parallel series of precipitous limestone ridges along a northwest to southeast direction. Climate varies with elevation, ranging from extremely dry to semi-dry and hot to subalpine climates at the highest elevations. Annual precipitation averages 400 to 900 mm (INEGI 1986).

We captured 10 adult Maroon-fronted Parrots (4 in 1999, 6 in 2000) during the breeding season

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TABLE 1. Vegetation types, area, and number of visits by Maroon-fronted Parrots during the nesting seasons 1999, 2000, and 2001 in the Sierra Madre Oriental, Mexico.

Vegetation type	Area used		
	1999	2000	2001
Pinus-Abies-Pseudotsuga	4,739 ha (n = 118)	29,350 ha (n = 28)	11,376 ha (n = 32)
Pinus	21,180 ha (n = 27)	3,504 ha (n = 37)	1,533 ha (n = 53)
Pinus cembroides	2,571 ha (n = 20)	2,849 ha (n = 3)	744 ha (n = 3)
Pinus-Quercus	744 ha (n = 3)	9,986 ha (n = 0)	4,581 ha (n = 0)
Chaparral	9,666 ha (n = 14)	1,957 ha (n = 213)	660 ha (n = 53)
Totals	38,900 ha (n = 182)	47,645 ha (n = 281)	18,894 ha (n = 141)

with mist nets at the El Taray Sanctuary in Coahuila and fitted them with telemetry neck-collars (Holohil Systems Ltd., Carp, ON, Canada). Radios weighed either 20 g (Model AI-2C, n = 9; loop antennas) or 13 g (Model SI-2C, n = 1; whip antenna) and represented 4.3 and 2.8% of average bird weight, respectively. Both types of transmitters had 24 months of expected battery life. The average (± SD) distance for signal detection was 3.6 ± 1.3 km (n = 181; Ortiz-Maciel 2000). These types of radios had no apparent negative impact on parrots (Snyder et al. 1994, Meyers 1996, Salinas-Melgoza and Renton 2005). We noted no apparent detrimental effects of transmitter attachment during our study, and some birds with non-functioning transmitters (dead batteries) were observed at the nesting cliffs in 2007.

We attempted to locate and follow radio-marked birds using 3-element yagi antennas and TRX-2000 receivers (Wildlife Materials Inc., Carbondale, IL, USA) to measure home ranges. We searched for parrots in high-elevation pine forests along valley roads during their breeding season, and also at nesting colonies and clay licks. We radio-located birds from dawn to sunset for 39 days from August to November 1999, 47 days from July to November 2000, and 43 days from May to October 2001.

We established a bird's position by recording the direction of the maximum signal, taking a bearing with a compass, and using a Global Positioning System (GPS) unit to ascertain the observer's location. Only one observer took bearings because of equipment limitations. We moved along the road >3 km and took another bearing to more precisely identify the location of a bird. We did not observe radio-marked birds directly at times, but usually heard vocalizations of parrot flocks, because daily tracking started at a roosting site. We also located parrots at nesting cliffs in their cavities. All bird locations were recorded on 1:50,000 scale maps of the Sierra Madre Oriental (McFarland 1991, Ortiz-Maciel 2000). Transmitter signals were not detected during all searches because parrots may have been out of the receiver's range and behind ridges that blocked the transmitter's signal.

Site Characterization.—We plotted all locations on a landscape image (from Landsat-TM 1993) and processed it with Arcview GIS 3.2 (ESRI 1999). Forest habitats, characterized following Hori-Ochoa (1998), were: *Pinus-Abies-Pseudotsuga*, *Pinus*, *Pinus cembroides*, *Pinus-Quercus*, *Quercus-Pinus*, and *Quercus*. Other habitats included submontane shrub, microphyllous desert shrub, desert shrub, chaparral, grassland, and agricultural zones.

We measured breeding home range size using the 50% kernel method for each field season (Worton 1989), and processed data using the Animal Movement extension from Arcview GIS 3.2 (ESRI 1999). We followed some parrots for an entire day and calculated total distances traveled by adding the distances between each location.

Habitat selection was estimated for each breeding season with a Chi-square independence test by counting the number of visits to each vegetation type and comparing the areal proportions for the 95% minimum convex polygon (White and Garrott 1990) (Table 1).

We calculated Bonferroni confidence intervals to identify use by vegetation types (Neu et al. 1974, Byers and Steinhorst 1984, White and Garrott 1990). Confidence intervals (95%) were calculated using only habitats where birds were observed including *Pinus-Abies-Pseudotsuga*, *Pinus*, *Pinus cembroides*, and *Pinus-Quercus* forest and chaparral. Values are presented as means

TABLE 2. Proportion of Maroon-fronted Parrot locations by habitat type, habitat available, and Bonferroni confidence intervals for the 1999, 2000, and 2001 breeding seasons, Sierra Madre Oriental, Mexico

Year and habitat type	Proportion of parrot locations (P_{obs})	Proportion of habitat available (P_{exp})	Bonferroni confidence intervals
1999			
Pinus-Abies-Pseudotsuga forest[a]	0.65	0.12	$0.56 \leq P_{obs} \leq 0.74$
Pinus forest	0.15	0.54	$0.08 \leq P_{obs} \leq 0.22$
Pinus cembroides forest	0.11	0.07	$0.05 \leq P_{obs} \leq 0.17$
Pinus-Quercus forest	0.02	0.02	$-0.01 \leq P_{obs} \leq 0.04$
Chaparral	0.08	0.25	$0.03 \leq P_{obs} \leq 0.13$
2000			
Pinus-Abies-Pseudotsuga forest	0.10	0.62	$0.05 \leq P_{obs} \leq 0.15$
Pinus forest[a]	0.13	0.07	$0.08 \leq P_{obs} \leq 0.18$
Pinus cembroides forest	0.01	0.06	$-0.01 \leq P_{obs} \leq 0.03$
Pinus-Quercus forest	0.00	0.21	$0.00 \leq P_{obs} \leq 0.00$
Chaparral[a]	0.76	0.04	$0.69 \leq P_{obs} \leq 0.82$
2001			
Pinus-Abies-Pseudotsuga forest	0.23	0.60	$0.14 \leq P_{obs} \leq 0.32$
Pinus forest[a]	0.38	0.08	$0.27 \leq P_{obs} \leq 0.48$
Pinus cembroides forest	0.02	0.04	$-0.01 \leq P_{obs} \leq 0.05$
Pinus-Quercus forest	0.00	0.24	$0.00 \leq P_{obs} \leq 0.00$
Chaparral[a]	0.38	0.04	$0.27 \leq P_{obs} \leq 0.48$

[a] Preferred habitat.

(± SD) with $P < 0.5$. The null hypothesis for each bird was that habitat types were used in accordance with their availability.

RESULTS

Home Range Size.—Home range size obtained with 50% kernel methods varied among breeding seasons. Home range size in 1999 was 12,379.05 ha ($n = 3$ birds), 8,633.82 ha ($n = 7$ birds) in 2000, and 4,736.75 ha ($n = 4$ birds) in 2001.

Daily Movements.—We observed two parrots in 1999 move a mean (± SD) distance of 23.6 ± 5.7 km per day ($n = 15$ days). The mean distance moved per day for three birds was 13.66 ± 7.64 km per day ($n = 6$ days) in 2000; the mean distance was 26.82 ± 18.17 km ($n = 5$ days) for two parrots in 2001. We also located a frequently-used communal night roost in Sierra La Viga.

Habitat Selection.—Maroon-fronted Parrots demonstrated preference for specific habitat types within the pine forest mosaic based on frequency of locations within 95% minimum convex polygon home ranges. There was a difference between habitat used and areal abundance (breeding seasons: 1999, $P < 0.001$, $X^2_4 = 493.5$; 2000, $P < 0.001$, $X^2_4 = 3{,}721.9$; 2001 $P < 0.001$, $X^2_4 = 688.4$). Bonferroni confidence intervals indicated some of the six forests habitats were used more than expected. *Pinus-Abies-Pseudotsuga* forest was used most in 1999, whereas *Pinus* forest and chaparral were used most in 2000 and 2001 (Table 2).

DISCUSSION

Most Maroon-fronted Parrot locations were at the highest elevations of the mountains, where subfreezing temperatures persist, indicating they are similar to Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*) and are temperate in their habitat preferences (Snyder et al. 1994, 1999). Breeding activity of Maroon-fronted Parrots started normally in 1999, but no young fledged and all nests failed by mid-September. Large home ranges that year reflected food scarcity similar to that reported for Thick-billed Parrots where breeding success and effort appeared tightly linked to food availability (Enkerlin-Hoeflich et al. 1999). Most used habitats were in high elevation *Pinus-Abies-Pseudotsuga* forest generally considered to be less suitable for foraging because the small reward ratio of small seeds characteristic of tree species in these forests (Enkerlin-Hoeflich et al. 1999).

Average home ranges of breeding Maroon-fronted Parrots were larger than those of other psittacines; juvenile Puerto Rican Amazon (*Ama-*

zona vittata) have estimated home ranges of 1,372 ha (Lindsey et al. 1991), Ground Parrots (*Pezoporus wallicus*) of Australia and Tasmania have estimated home ranges of 9.2 ha (McFarland 1991), and juvenile Lilac-crowned Amazon (*Amazona finschi*) have home ranges of 4,674 ha (Salinas-Melgoza 2003). These home range differences may reflect that Maroon-fronted Parrots now inhabit disturbed areas and require larger areas to satisfy their basic needs. Continental parrot species have larger home ranges, compared with island species, because of more availability of habitats assuring refuge during periods of stress (Snyder et al. 1987).

Maroon-fronted Parrots did not use all forest types equally; all of their activities were in five habitats (4 forest types and chaparral). *Pinus-Abies-Pseudotsuga* forest was used more than expected in 1999, whereas *Pinus* forest and chaparral were more used than expected in 2000 and 2001. The El Taray nesting cliff is in chaparral habitat which may influence apparent habitat preferences.

The dependence of Maroon-fronted Parrots on coniferous forests increases their vulnerability with respect to habitat changes resulting from timber harvest and fires as noted >25 years ago (Lawson and Lanning 1981, Enkerlin-Hoeflich et al. 1999). These temperate forests support different vegetation types and regeneration, management, or restoration varies depending on each plant community. For example, after a fire, chaparral stands of 20–30 years in age have nearly complete shrub cover with few to no emergent trees (Brown et al. 2000). Thus, the overall productivity of habitats for parrots is decreasing given the slow or absent forest regeneration and replacement by oak chaparral with little food value for parrots. Spatial and temporal patchiness of food plants may be increasing which may lead to food-induced stress on the population. Maroon-fronted Parrots also have local pressure for one of their preferred food sources, pinion pine seeds, which are valuable at the local market and extensively harvested as an income supplement by rural families.

Recent fires have devastated several important sites, including foraging and breeding areas; >90% of standing trees died in 1998 in an area of 5,000 ha (Brown et al. 2000). Another fire in 2006 destroyed 545 ha of standing trees (CONAFOR 2006a, b) including >70% of the El Taray Sanctuary (Manzano-Camarillo 2006). These habitat changes have directly affected Maroon-fronted Parrot nesting activities.

Regional forest managers should conserve and re-establish *Pinus* forest communities. Management should include control of timber harvests, fires, reforestation, and restoration (Valdez-Tamez 1981). Forest management should be implemented to manage and conserve critical habitats, increase size of forested areas, and provide alternative livelihood opportunities for local inhabitants via ecotourism or provision of payment and incentives for ecosystem services and watershed protection.

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SHORT-TERM EFFECTS OF FIRE ON BREEDING BIRDS IN SOUTHERN APPALACHIAN UPLAND FORESTS

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ABSTRACT.—We investigated how variation in fire severity (control or no fire; low, medium, and high severity fires) and interval (1–2 years vs. 3–6 years after fires) affected habitat and avian abundance, species diversity, richness, and evenness in the southern Appalachian Mountains. Fire severity and interval had significant implications for both habitat and avian communities. Species richness within 2 years of fires was on average 26% higher in areas receiving medium and high severity treatments than in unburned control units. Species diversity and species richness were markedly greater 3–6 years after fires within high severity treatments (12 and 44%, respectively), compared to unburned controls. Relative abundance and species evenness did not vary with fire severity or time since fire. The short-term effects of low severity fires, or high severity fires with short rotation periods (≤2 years) may have limited positive effects on avian communities. Facilitation of disturbance regimes including mid to high severity fires, which foster uneven-aged forests, can be an effective conservation tool for restoring avian communities. *Received 30 June 2009. Accepted 1 March 2010.*

Disturbance is a fundamental ecological process that has had a role in structuring and maintaining diversity within many ecological communities (Loucks 1970, Elliott et al. 1999, Brawn et al. 2001, Bond and Keeley 2005, Bond et al. 2005). Generally, disturbance increases diversity by creating a mosaic of habitats or successional stages within a landscape (Askins 2001, Brawn et al. 2001). Fire is one form of disturbance that has had a large part in structuring the ecological communities of the southern Appalachian Mountains (Lorimer 1980, Van Lear and Waldrop 1989, Waldrop et al. 1992). Suppression of fire on public lands during the past century has likely reduced diversity and structure of animal and plant communities (Abrams 1992, Lorimer 2001, Artman et al. 2005). Several federal land management agencies, in an effort to restore diversity and ecological function, now plan for increased use of prescribed fire in the southern Appalachian Mountains. However, effects of restoring fire on wildlife are largely unknown in these mostly hardwood forest systems. In particular, effects of varying fire severity and interval on wildlife are largely unknown.

Many bird species associated with early succession habitats and pine (*Pinus* spp.) savannas would likely benefit from return of fire to the southern Appalachian Mountains. Species of concern include: Bachman's Sparrow (*Aimophila aestivalis*), Northern Bobwhite (*Colinus virginianus*), Red-cockaded Woodpecker (*Picoides borealis*), Prairie Warbler (*Dendroica discolor*), and Golden-winged Warbler (*Vermivora chrysoptera*) (Brewster 1886, Burleigh 1958, Stupka 1963, Hunter et al. 2001, Klaus 2004). Measured responses for other bird species may not be positive (Lang et al. 2002, Artman and Downhower 2003, Tomcho et al. 2006), and the benefits of fire restoration may not integrate similarly across all members of avian communities, or in all habitats (Artman et al. 2001, Saab and Powell 2005, Tomcho et al. 2006, Greenberg et al. 2007). Thus, reintroduction of fire should be based on desired ecological condition.

The historical suppression of fire and changes in agricultural practices within the eastern United States have been implicated in loss of early successional habitat (Askins 2001). Loss of this habitat type has had a significant impact on avian communities. Early succession songbirds in the southern Appalachians have the strongest declines of any group of birds (Hunter et al. 1999, Sauer et al. 2005). Many of the species that require mature forest for nesting also use early succession habitat as fledglings and during molt (Anders et al. 1998, Vega Rivera et al. 1999, Marshall et al. 2003, Rush and Stutchbury 2008). Restoration of early successional habitat may be a key feature of policies directed at conservation of many avian species (Dettmers 2003, Bulluck and Buehler 2006, Buehler et al. 2007).

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Prescribed fire is often cited as a likely tool for restoring and providing suitable habitat for many avian species (Partners in Flight Working Group 2002), but our current understanding of the appropriate application of fire in shaping forest ecosystems of the southern Appalachian Mountains remains limited. We currently know of only a few studies that have examined the effects of prescribed fire on songbirds in hardwood forests of the eastern United States (Aquilani et al. 2000; Artman et al. 2001, 2005; Greenberg et al. 2007); only one of these studies occurred in the southern Appalachians. Our objectives were to document how breeding season distributions of birds changed with variation in fire severity and time since fire in the southern Appalachians.

METHODS

Study Area.—This study was conducted within the Brasstown and Tallulah ranger districts of the Chattahoochee-Oconee National Forest (CNF), Murray County, Georgia, USA. U.S. Forest Service (USFS) personnel were consulted within the CNF and 22 potential study sites were identified at elevations from 600 to 1,500 m. All burn units were >200 ha and had burned in the last 8 years, either as a prescribed fire or as part of a wildfire. Vegetation sampling sites were placed into one of three fire severity groups on the basis of the extent of canopy mortality: low, medium, or high. Low severity burns were typical of most 'fuel reduction' prescribed fires in the southern Appalachians. Flame lengths were generally less than 1 m, resulting in <5% canopy mortality throughout the burn unit and low to moderate midstory mortality. Moderate to severe midstory and 5 to 20% canopy mortality characterized medium severity burns and flame lengths ranged from <0.5 m in mesic sites to 4 m along dry ridge tops, leaving a heterogeneous result. High severity burns were characterized by 20 to 50% canopy mortality, mostly along ridge tops, and severe to total midstory mortality except in ravines.

We selected 12 of the 22 burn units, four of each treatment, based on similarity of forest type, elevation, and average aspect. All chosen burn units had been burned ≤6 years earlier. Half the 12 burn units selected (2 of each treatment) were in sites that were burned <2 years previously, and two were in sites that were burned 3–6 years previously. Forest types consisted primarily of mixed pine (*Pinus* spp.)-hardwoods and drier oak-hickory (*Quercus-Carya*), although ridge tops occasionally included small stands of *P. taeda*, *P. virginiana*, *P. rigida*, and *P. pungens*. Four control units were also identified with the aid of USFS personnel. Control units were similar in forest type, elevation, and average aspect but had not burned in ≥20 years.

Bird Surveys.—Surveys were conducted by USFS and Georgia Department of Natural Resources staff. Participants received several weeks of spring training on bird identification and point-count techniques prior to surveys. All participants had conducted bird surveys for several years prior to this study. Two transects were placed for each survey within each burn unit. Transects followed contours and were at least 200 m apart. All surveys were conducted between 0630 and 1100 hrs, 17 May–10 June 2004, following protocols established by Hamel et al. (1996), except that counts were conducted for 10 min and distance bands of 0–10, 11–25, 26–50, 51–100, and >100 m were used. Ten point counts were conducted on each survey transect, 20 per burn unit. Locations of individual point counts were: (1) separated by at least 200 m, (2) at least 100 m inside the burn unit, and (3) placed in upland mixed pine hardwood stands or oak stands. Ravines, road edges, and other cover types were avoided. Four replications of each treatment were surveyed for a total of 80 points per treatment.

Habitat Measurements.—We conducted variable-radius vegetation surveys within each burn unit centered on each point count location. We measured the basal area using a 10-factor prism of live trees >25 cm diameter breast height (DBH); this metric is referred to as BASAL AREA. We visually estimated average canopy (CANOPY COVER) and herbaceous cover (HERBACEOUS COVER) to the nearest 10% for a 25-m radius around each plot center. We also measured shrubs (woody plants 1 to 7 m tall and <12 cm DBH) within a 3-m radius around the plot center by counting all stems (SHRUB DENSITY) and measuring average shrub height (SHRUB HEIGHT) to the nearest decimeter. Each burn unit was categorized based on known fire histories into one of three fire histories: (1) control [not burned within the last ≥20 years], (2) burned within 1–2 years of surveys, and (3) burned within 3–6 years of surveys.

Data Analysis.—We restricted our analysis to limit the repeated counting of the same individual at two adjacent survey sites and to include only those birds detected within 100 m of each survey

point. The relative abundance of each species for each treatment was calculated as the average number of individuals detected/ha. We restricted each point-count survey to counts of individuals detected per distance band during each time interval for conservative estimates of relative abundance of each species. Detections of the same species in the same distance band but in different time intervals were treated as a possible recount of the same individual and were excluded from further analysis. All bird species observed at each survey point along each transect were used in calculations of bird species diversity, species richness, and species evenness. Species diversity was calculated as the Shannon-Weaver Diversity Index (H') (Shannon and Weaver 1963). Species richness was calculated as the number of individual species observed per point during each point count, and species evenness was calculated as H' divided by the natural log of species richness (Magurran 1988).

We used linear, mixed-effects models (*lme*) in R (Version 2.7.1; R Development Core Team 2008) to compare habitat measurements, diversity, species evenness, and species richness between treatments using the burn unit as the experimental unit. Mixed-effects models are appropriate for this data structure because they partition information into multi-level components. The data recommends level-1 (survey point), level-2 (survey transect), and level-3 (burn unit) components in our case. Each component is estimated with the appropriate degrees of freedom, and the standard errors of other parameter estimates are appropriately adjusted (Raudenbush and Bryk 2002). Transect and burn unit effects were accounted for as random variables, and treatment as a fixed effect. We used q-q plots prior to analysis to examine the normality of each habitat metric. We log transformed BASAL AREA, SHRUB DENSITY, SHRUB HEIGHT, and HERBACEOUS COVER and arcsine square-root transformed CANOPY COVER to improve normality and homoscedasticity. We used conditional *t*-tests for each *lme* to ascertain whether covariates were significantly different from zero (Pinheiro and Bates 2000). We also developed a series of orthogonal contrasts to compare means between the different levels of burn severity and times since fire.

We used canonical correspondence analysis (CCA) of data collected at each of the survey points to examine the relationship between bird community structure and measured environmental variables (McCune and Grace 2002). This technique was used to produce graphical presentations depicting relationships among abundance of individual species, treatments, and measured environmental gradients. Habitat variables explaining a significant amount of variation ($P \leq 0.10$), as calculated by Monte Carlo permutation tests (1,000 random permutations of samples in the species data; package Vegan in R) (R Development Core Team 2008), were included in the CCA analyses. The means of these variables are represented by the origin in the resulting diagram. We constrained our analysis for clarity in presentation of bird assemblages to include only those species that were detected at ≥20% of all survey points. We conducted two separate analyses to facilitate comparisons, one comparing habitat and bird assemblage between control and treatments 1–2 years after fires, and a separate analysis with similar comparisons for control and treatments sampled 3–6 years after fires. We log transformed BASAL AREA, SHRUB DENSITY, SHRUB HEIGHT, and HERBACEOUS COVER and arcsine square-root transformed CANOPY COVER prior to using them in the CCA.

RESULTS

Fire and Habitat.—Fire severity affected habitat structure. Comparisons of treatments and unburned controls revealed CANOPY COVER and SHRUB DENSITY differed among treatments ($F_{6,9} = 19.1$, $P < 0.001$; $F_{6,9} = 4.0$, $P = 0.03$, respectively), (Fig. 1). High severity treatments had significantly less CANOPY COVER than control units both 1–2 years ($t = 6.8$, df = 9, $P < 0.001$), and 3–6 years after fires ($t = 7.9$, df = 9, $P < 0.001$). CANOPY COVER did not differ relative to the number of years since fires ($t = 1.0$, df = 9, $P = 0.33$) but, SHRUB DENSITY was significantly lower among high severity treatments 1–2 years after fires than 3–6 years after fires ($t = -4.4$, df = 9, $P = 0.002$).

Effects on Avian Diversity and Communities.—Sixty-three species were detected among the four treatments (Table 1). Species richness differed among several treatments ($F_{6,9} = 4.9$, $P = 0.02$) and was significantly higher 1–2 years after fires relative to the low severity burn units. It did not differ among medium and high severity burn units ($t = -2.5$, df = 9, $P = 0.03$, $t = -2.3$, df = 9, $P = 0.05$) (Fig. 2). Species richness 3–6 years

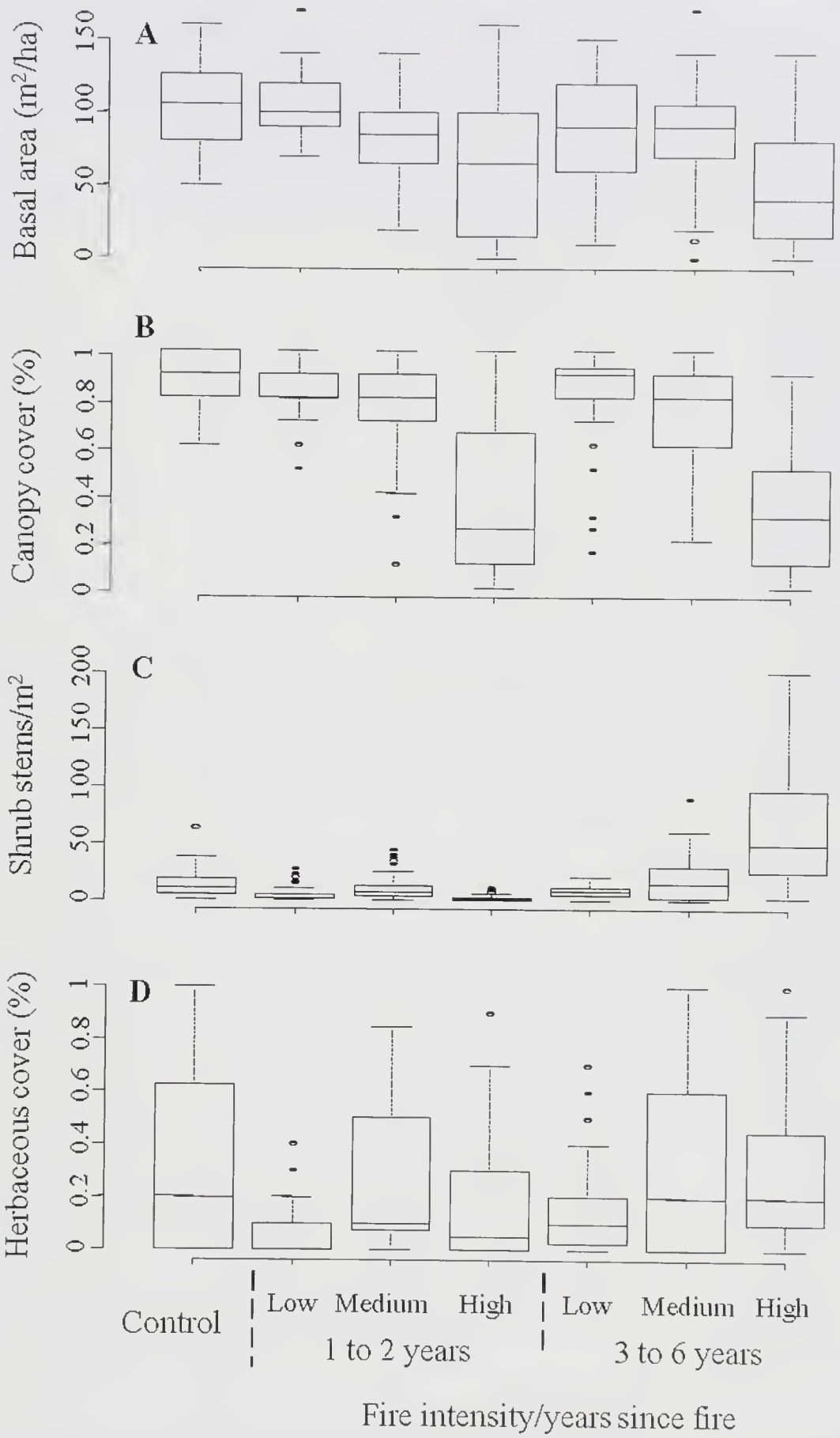

FIG. 1. Box and whisker plots of habitat characteristics measured at point-count locations within control and burn treatments. Whiskers represent maximum and minimum observations while boxes represent the 25 and 75% quartiles.

TABLE 1. Relative abundance of species detected during surveys in the southern Appalachian Mountains. Estimates are individuals/10ha ($\bar{x} \pm$ SE). Missing values indicate species not detected.

Species	Treatment (years after fires)						
		Low		Medium		High	
Scientific name	Control	1–2	3–6	1–2	3–6	1–2	3–6
Ruffed Grouse *Bonasa umbellus*		0.1 ± 0.1					
Wild Turkey *Meleagris gallopavo*		0.2 ± 0.1					0.1 ± 0.1
Black Vulture *Coragyps atratus*							0.2 ± 0.2
Turkey Vulture *Cathartes aura*				0.2 ± 0.2			0.3 ± 0.2
Sharp-shinned Hawk *Accipiter striatus*			0.2 ± 0.2				
Broad-winged Hawk *Buteo platypterus*		0.3 ± 0.2	0.2 ± 0.2	0.1 ± 0.1		0.1 ± 0.1	
Red-tailed Hawk *B. jamaicensis*					0.2 ± 0.1		
Mourning Dove *Zenaida macroura*	0.1 ± 0.1	0.3 ± 0.2	0.3 ± 0.2	0.2 ± 0.1	0.6 ± 0.2	0.7 ± 0.2	1.0 ± 0.3
Yellow-billed Cuckoo *Coccyzus americanus*			0.3 ± 0.2	0.2 ± 0.1	0.5 ± 0.2	0.3 ± 0.2	0.5 ± 0.2
Barred Owl *Strix varia*	0.1 ± 0.1						
Chimney Swift *Chaetura pelagica*	0.1 ± 0.1		0.3 ± 0.2	0.6 ± 0.2	0.2 ± 0.2	1.2 ± 0.4	0.6 ± 0.3
Ruby-throated Hummingbird *Archilochus colubris*			0.1 ± 0.1		0.1 ± 0.1		0.1 ± 0.1
Red-bellied Woodpecker *Melanerpes carolinus*						0.1 ± 0.1	
Downy Woodpecker *Picoides pubescens*			0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Hairy Woodpecker *P. villosus*	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.6 ± 0.2	0.1 ± 0.1	1.2 ± 0.3	0.6 ± 0.2
Northern Flicker *Colaptes auratus*			0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.7 ± 0.3	0.4 ± 0.2
Pileated Woodpecker *Dryocopus pileatus*	0.9 ± 0.3	1.6 ± 0.3	1.1 ± 0.2	1.5 ± 0.4	1.6 ± 0.3	1.3 ± 0.3	1.5 ± 0.3
Eastern Wood-Pewee *Contopus virens*				0.7 ± 0.2	0.2 ± 0.2	1.4 ± 0.3	2.4 ± 0.4
Eastern Phoebe *Sayornis phoebe*			0.1 ± 0.1		0.1 ± 0.1	0.2 ± 0.1	
Great Crested Flycatcher *Myiarchus crinitus*	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.5 ± 0.2	0.6 ± 0.2

TABLE 1. Continued.

Species Scientific name	Treatment (years after fires)						
		Low		Medium		High	
	Control	1–2	3–6	1–2	3–6	1–2	3–6
Yellow-throated Vireo *Vireo flavifrons*				0.2 ± 0.1			0.4 ± 0.2
Blue-headed Vireo *V. solitarius*	0.6 ± 0.2	0.1 ± 0.1	1.0 ± 0.3	0.7 ± 0.2	0.7 ± 0.2	1.3 ± 0.3	0.7 ± 0.2
Red-eyed Vireo *V. olivaceus*	5.6 ± 0.4	4.0 ± 0.5	4.4 ± 0.5	4.0 ± 0.5	5.8 ± 0.5	3.5 ± 0.6	5.4 ± 0.5
Blue Jay *Cyanocitta cristata*	0.9 ± 0.3	0.6 ± 0.2	0.9 ± 0.3	0.9 ± 0.3	0.6 ± 0.2	0.6 ± 0.2	0.8 ± 0.3
American Crow *Corvus brachyrhynchos*	1.5 ± 0.3	4.6 ± 0.6	3.7 ± 0.4	1.3 ± 0.3	1.4 ± 0.3	1.3 ± 0.3	2.7 ± 0.4
Carolina Chickadee *Poecile carolinensis*		0.3 ± 0.2	0.5 ± 0.2	0.2 ± 0.1	0.7 ± 0.3	0.1 ± 0.1	0.4 ± 0.2
Tufted Titmouse *Baeolophus bicolor*	1.0 ± 0.2	1.4 ± 0.2	2.5 ± 0.4	1.7 ± 0.3	1.6 ± 0.3	0.6 ± 0.3	2.1 ± 0.3
White-breasted Nuthatch *Sitta carolinensis*	0.5 ± 0.2	0.2 ± 0.1	0.4 ± 0.2	0.4 ± 0.2	0.5 ± 0.3	0.6 ± 0.3	0.5 ± 0.2
Carolina Wren *Thryothorus ludovicianus*	0.2 ± 0.1	0.3 ± 0.2	0.2 ± 0.1	0.6 ± 0.2	0.4 ± 0.2	1.3 ± 0.3	1.4 ± 0.3
Blue-gray Gnatcatcher *Polioptila caerulea*	0.1 ± 0.1			0.2 ± 0.1	0.1 ± 0.1		0.6 ± 0.3
Wood Thrush *Hylocichla mustelina*	0.1 ± 0.1	0.6 ± 0.3	0.2 ± 0.1	0.2 ± 0.1	0.6 ± 0.3	0.4 ± 0.2	0.3 ± 0.2
Brown Thrasher *Toxostoma rufum*					0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Cedar Waxwing *Bombycilla cedrorum*				0.1 ± 0.1		0.9 ± 0.5	0.2 ± 0.2
Golden-winged Warbler *Vermivora chrysoptera*					0.2 ± 0.2		
Northern Parula *Parula americana*				4.0 ± 0.4			0.1 ± 0.1
Chestnut-sided Warbler *Dendroica pensylvanica*	0.4 ± 0.2		0.2 ± 0.2	1.4 ± 0.4	0.8 ± 0.2	1.5 ± 0.4	6.6 ± 0.5
Black-throated Blue Warbler *D. caerulescens*			0.6 ± 0.3	1.0 ± 0.3			
Black-throated Green Warbler *D. virens*	1.1 ± 0.3	1.2 ± 0.3	1.7 ± 0.4	1.4 ± 0.3	3.5 ± 0.5	0.8 ± 0.2	1.0 ± 0.3
Blackburnian Warbler *D. fusca*	0.4 ± 0.2			0.9 ± 0.3	0.3 ± 0.2		0.4 ± 0.2
Yellow-throated Warbler *D. dominica*	0.1 ± 0.1	0.1 ± 0.1	0.9 ± 0.3		0.2 ± 0.1		0.8 ± 0.3

TABLE 1. Continued.

Species Scientific name	Treatment (years after fires)						
		Low		Medium		High	
	Control	1–2	3–6	1–2	3–6	1–2	3–6
Pine Warbler *D. pinus*	0.2 ± 0.1		0.2 ± 0.1			0.3 ± 0.1	0.2 ± 0.1
Prairie Warbler *D. discolor*						0.1 ± 0.1	1.0 ± 0.3
Cerulean Warbler *D. cerulea*							0.2 ± 0.2
Black-and-white Warbler *Mniotilta varia*	1.8 ± 0.3	0.6 ± 0.2	1.4 ± 0.3	1.5 ± 0.3	1.3 ± 0.3	1.0 ± 0.2	0.9 ± 0.3
American Redstart *Setophaga ruticilla*	0.1 ± 0.1				0.1 ± 0.1		0.6 ± 0.2
Worm-eating Warbler *Helmitheros vermivorum*	0.6 ± 0.2	0.3 ± 0.2	0.3 ± 0.2	0.1 ± 0.1	0.5 ± 0.2		0.2 ± 0.2
Ovenbird *Seiurus aurocapilla*	4.7 ± 0.5	1.1 ± 0.3	2.3 ± 0.5		2.9 ± 0.4	1.2 ± 0.3	0.2 ± 0.2
Kentucky Warbler *Oporornis formosus*	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1		0.1 ± 0.1
Common Yellowthroat *Geothlypis trichas*							0.1 ± 0.1
Hooded Warbler *Wilsonia citrina*	0.9 ± 0.3	1.8 ± 0.3	2.5 ± 0.4	0.6 ± 0.2	1.3 ± 0.3		1.4 ± 0.4
Canada Warbler *W. canadensis*				0.2 ± 0.1			
Yellow-breasted Chat *Icteria vireos*	0.2 ± 0.2				0.1 ± 0.1		2.9 ± 0.5
Eastern Towhee *Pipilo erythrophthalmus*	0.5 ± 0.2	0.4 ± 0.2	1.4 ± 0.4	0.8 ± 0.2	0.9 ± 0.3	4.2 ± 0.5	4.0 ± 0.5
Chipping Sparrow *Spizella passerina*						1.2 ± 0.4	0.2 ± 0.1
Field Sparrow *S. pusilla*							0.1 ± 0.1
Song Sparrow *Melospiza melodia*							0.1 ± 0.1
Dark-eyed Junco *Junco hyemalis*			0.1 ± 0.1	0.2 ± 0.1			
Scarlet Tanager *Piranga olivacea*	1.2 ± 0.3	1.4 ± 0.3	2.4 ± 0.5	1.9 ± 0.3	2.4 ± 0.4	2.6 ± 0.4	2.3 ± 0.4
Northern Cardinal *Cardinalis cardinalis*	0.1 ± 0.1	0.3 ± 0.2	0.8 ± 0.2		0.1 ± 0.1	0.1 ± 0.1	0.6 ± 0.2
Rose-breasted Grosbeak *Pheucticus ludovicianus*	0.2 ± 0.1			0.4 ± 0.2	0.3 ± 0.2		0.6 ± 0.2

TABLE 1. Continued.

Species	Treatment (years after fires)						
		Low		Medium		High	
Scientific name	Control	1–2	3–6	1–2	3–6	1–2	3–6
Blue Grosbeak				0.4 ± 0.2			
Passerina caerulea							
Indigo Bunting	1.0 ± 0.3	0.7 ± 0.3	2.5 ± 0.5	2.6 ± 0.4	2.1 ± 0.3	4.0 ± 0.4	5.3 ± 0.6
P. cyanea							
American Goldfinch				0.1 ± 0.1	0.1 ± 0.1	1.0 ± 0.3	0.6 ± 0.3
Spinus tristis							

after fires, relative to all other treatments, was significantly higher among the high severity burn units (Fig. 2). Generally, species diversity (H') did not differ among treatments or relative to time since fire ($F_{6,9} = 2.4$, $P = 0.12$). However, species diversity was significantly greater in the high severity burn units 3–6 years after fires in contrast with the controls ($t = -3.0$, df = 9, $P = 0.1$) (Table 2). Species evenness did not differ among treatments ($F_{6,9} = 0.43$, $P = 0.84$) (Fig. 2).

Canonical correspondence analysis for bird species assemblages and habitat measured 1–2 years after fires indicated the overall relationship between species and environmental variables (all canonical axes) differed significantly from those derived randomly (Table 2). The primary axis (horizontal axis, Fig. 3) indicated strong positive relationships with BASAL AREA, SHRUB DENSITY, and CANOPY COVER, a moderate positive effect with SHRUB HEIGHT, and a moderate negative effect with HERBACEOUS COVER (Table 2). The secondary axis (vertical axis, Fig. 3), indicated a strong negative relationship with SHRUB HEIGHT and weaker relationships with SHRUB DENSITY, CANOPY COVER, and BASAL AREA. The habitat in high severity burn units 1–2 years after fires was best characterized by reduced CANOPY COVER and BASAL AREA (Fig. 3).

The avian community associated with high severity burn units 1–2 years after fires was largely represented by early successional species including American Goldfinch (scientific names are in Table 1), Eastern Towhee, Indigo Bunting, and Eastern Wood-Pewee. These species were along the negative side of the primary axis. Ovenbirds, a species most closely associated with habitat characterized by higher CANOPY COVER, BASAL AREA, and HERBACEOUS COVER tended to be in a positive position relative to both the primary and secondary axes. Treatment ellipses overlapped among other species indicating that habitat metrics and species pools were similar among treatments (Fig. 3).

Relationships between species and habitat 3–6 years after fires were significantly different for all variables except SHRUB HEIGHT (Table 2). This metric was omitted from further analysis. The primary axis of the CCA had a strong negative relationship with BASAL AREA and CANOPY COVER, and a strong positive relationship with SHRUB DENSITY. The secondary axis had a strong negative relationship with HERBACEOUS COVER. High severity burn units were best characterized by habitat with less CANOPY COVER, lower BASAL AREA, and higher SHRUB DENSITY. Several species along the primary axis were depicted farthest from the centroid and included Yellow-breasted Chat, Chestnut-sided Warbler, Indigo Bunting, and Eastern Towhee (Fig. 4). Species such as Hooded, Black-and-White, and Black-throated Green warblers were mapped highest on the vertical axis (Fig. 4).

DISCUSSION

The effects of fire severity can vary between species and across avian communities. Our results indicated both species richness and diversity increased relative to fire severity and time since fire. Relative abundance did not change considerably among treatments or with time since fire (Table 1, Fig. 2); this may have been a bias from our conservative analysis of repeat observations. Species evenness also remained stable among treatments.

The species most negatively affected by fire was the Ovenbird, which is associated with closed

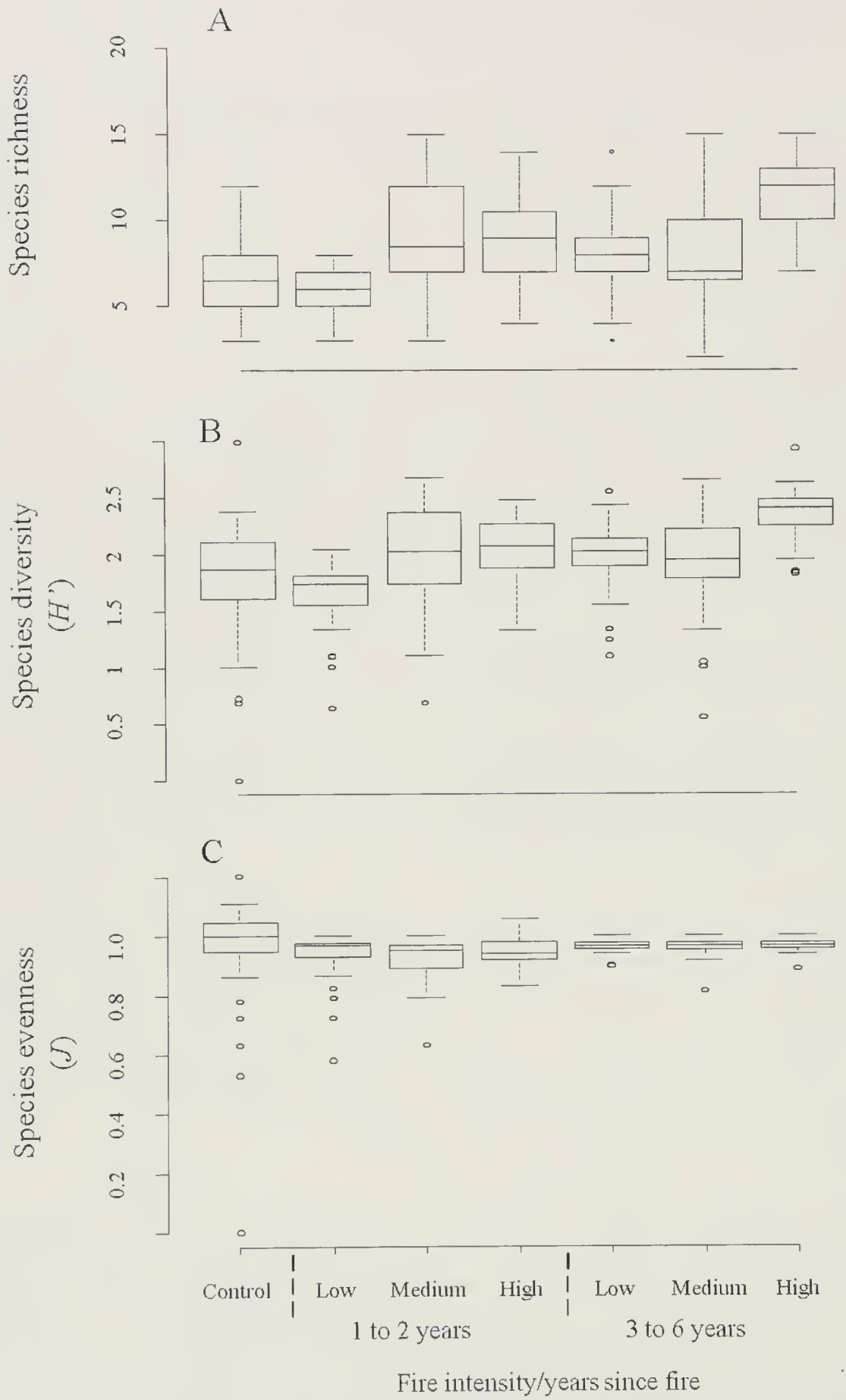

FIG. 2. Species richness, diversity, and evenness among avian communities within the southern Appalachian Mountains. Surveys were conducted at sites which received one of four levels of fire severity <2 years since fire or 3–6 years after fire.

TABLE 2. Values for the first two axes in canonical correspondence analysis (CCA) and correlations with environmental variables used to constrain the ordination. CCA was based on estimates of relative avian abundance and habitat measured at control (no fire) and varying levels of fire severity treatments within 2 years and 3 to 6 years after fires in the southern Appalachian Mountains.

Statistic	1–2 years post fire				3–6 years post fire			
	CCA Axis I	CCA Axis II	*r*	*P*	CCA Axis I	CCA Axis II	*r*	*P*
Eigenvalues	0.34	0.28			0.33	0.16		
Cumulative variance	0.18	0.33			0.23	0.33		
Intraset correlations								
BASAL AREA	0.95	−0.30	0.23	<0.001	−1.00	−0.013	0.16	<0.001
SHRUB HEIGHT	0.59	−0.80	0.19	<0.001	0.23	0.97	0.00	0.94
SHRUB DENSITY	0.93	−0.37	0.05	0.02	0.89	−0.45	0.20	<0.001
HERBACEOUS COVER	−0.58	0.82	0.04	0.07	0.12	−0.99	0.37	0.063
CANOPY COVER	0.96	−0.28	0.25	<0.001	−0.99	0.11	0.04	<0.001

canopy forests with limited understory (Neimi and Hanowski 1984, Smith and Shugart 1987). Availability of this habitat may be reduced for many years following a high severity fire, a relationship governed by increased growth of herbaceous cover and lack of canopy protection (Elliott et al. 1999, Greenberg et al. 2007). Conversely, our results indicated that many

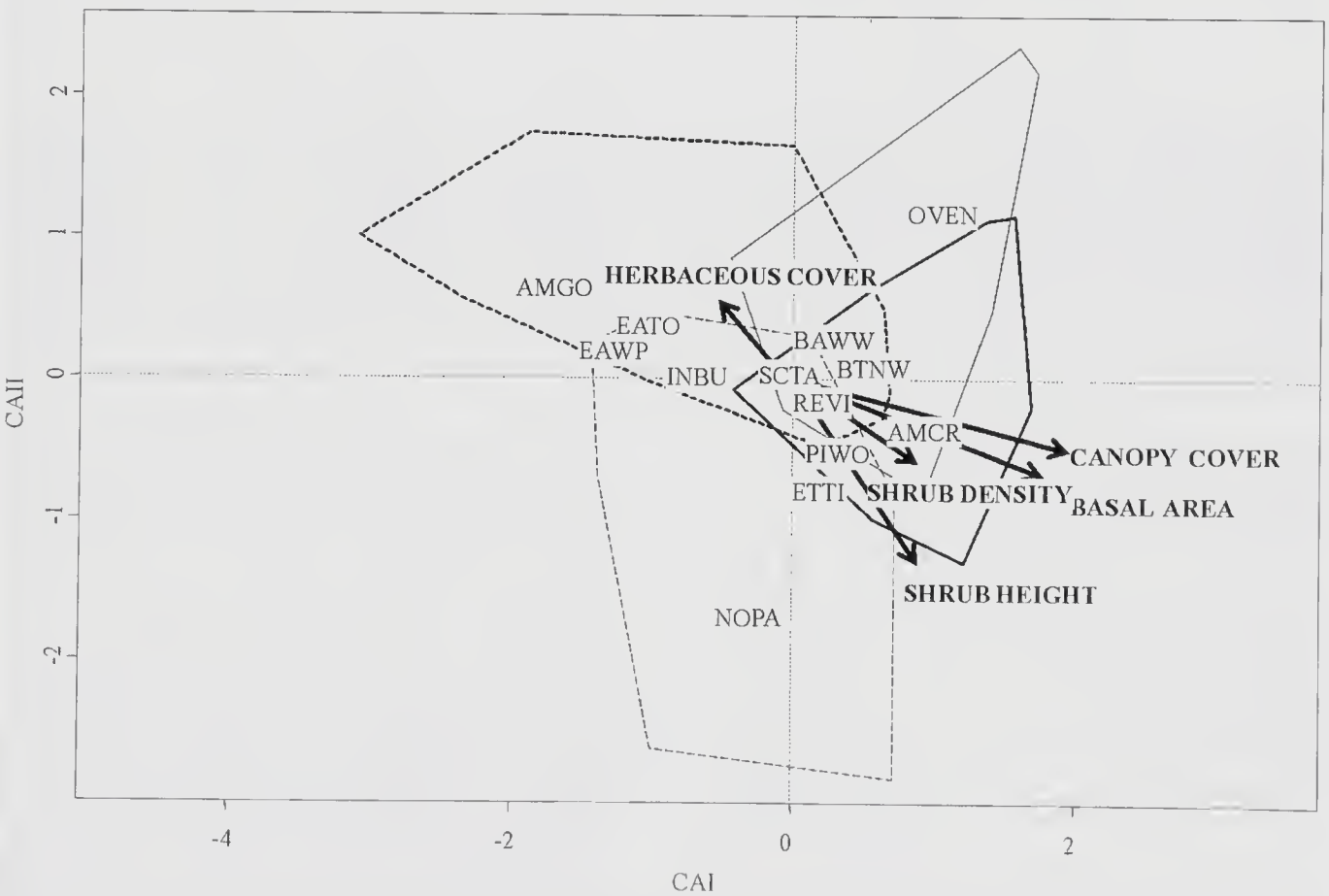

FIG. 3. Habitat associations relative to fire severity for species (AMGO = American Goldfinch, etc.) detected on point-count surveys 1–2 years after fires in northern Georgia. Solid line represents boundary of habitat centroids measured using linear combination scores derived for control units (no fire, thin solid line), low severity (thick solid line), medium severity (thin dashed line), and high severity burn units (thick dashed line). Boxed habitat metrics are mapped with arrows indicating relative locations within the community. The longer the distance between the metric and the community center (axis point 0, 0) the stronger the relationship with the community. Proximity of individual species to habitat metrics indicates strength of association between relative species abundance and habitat metric. Only those species detected on ≥20% of surveys are shown.

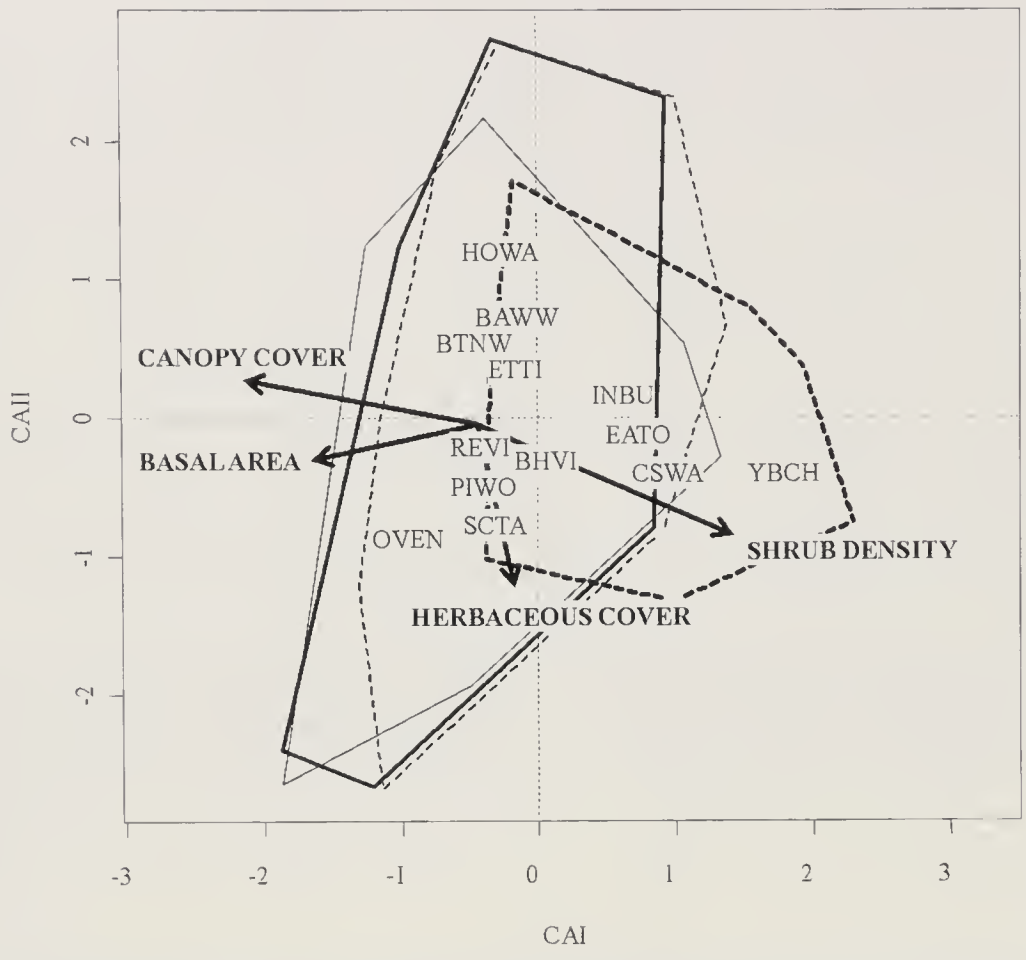

FIG. 4. Habitat associations relative to fire severity for species (BAWW = Black and White Warbler, etc.) detected on point-count surveys conducted 3–6 years after fires in northern Georgia. Community mapped using Canonical Correspondence Analysis (CCA) with habitat centroids based on linear combination scores derived from habitat measured at control units (thin solid line), low severity (thick solid line), medium severity (thin dashed line), and high severity (thick dashed line). Boxed habitat metrics are mapped with arrows indicating relative locations within the community. The longer the distance between the metric and the community center (axis point 0, 0) the stronger the relationship with the community. Proximity of individual species to habitat metrics indicates strength of association between relative abundance and habitat metric. Only those species detected on ≥20% of surveys are shown.

species associated with disturbance and early successional habitat responded positively to fire severity.

Species that responded positively to increased fire severity included American Goldfinch, Chestnut-sided Warbler, Eastern Towhee, Indigo Bunting, Prairie Warbler, and Yellow-breasted Chat. Most of these species had higher abundance 3–6 years after fires, tracking decreased canopy cover and released growth of shrubs relating to increased shrub density. Also included among these species were Golden-winged and Cerulean warblers, species that are both endangered in Georgia. Both species were encountered once and were found exclusively in either medium (Golden-winged Warbler) or high severity (Cerulean Warbler) treatments (Table 1).

The physiognomic properties of habitats continued 3–6 years after high severity fires. Continued canopy openness related positively with abundance of several woodpecker species; Hairy Woodpeckers and Northern Flickers had highest abundance in high severity treatments. Species characteristic of forests with more-open canopy, such as Yellow-billed Cuckoo, Eastern Wood-Pewee, and Blue-gray Gnatcatchers increased relative to fire severity, responses that may relate to suppressed understory, more-open conditions, higher insect abundance, and improved foraging habitat (Greenberg et al. 2007).

Mid-story nesting species are thought to be relatively flexible in habitat selection and may not respond to fire-driven habitat change (Artman et al. 2005). Our results indicated density of several of these mid-story nesting species including Wood Thrush, Blue-headed Vireo, and Red-eyed Vireo did not differ relative to either fire severity or time since fire. However, American Redstart, a species that forages and nests in shrubs and vines, appeared to be absent from treatment burn units

during the first 2 years after fires. This association may reflect the temporary reduction of vertical structure during the first few years after a fire (Waldrop et al. 2007).

Uneven-age forests may represent natural historical conditions within the southern Appalachian Mountains (Lorimer 1980). Our results indicated that returning a fire regime to these forests may be an effective conservation tool for restoring avian diversity (Artman et al. 2005, Greenberg et al. 2007). However, effectiveness of fire restoration can vary (Artman et al. 2005). Continued fire suppression, or frequent application of low severity fires, may lead to forest maturation, have limited effects on species diversity, and can lead to declines in some species (Artman et al. 2005, Klaus et al. 2005). Application of high severity fires corresponding with short rotation periods may not allow habitat regeneration and can lead to decreased diversity. Application of higher severity fires over broader time intervals may be more effective in managing uneven-age forests.

Changes in relative abundance of a particular species may not equate directly with habitat quality or persistence (Johnson 2007). We did not examine the effects of treatment on reproductive success, survival, or other demographic measures and cannot provide predictions relating treatments to these population metrics. Our results reflect acute numerical relationships among individual species and across avian communities. Longer-term studies focused on addressing variation in population demographics through several seasons after different fire severity treatments would greatly benefit our understanding of avian communities.

CONSERVATION IMPLICATIONS

Management directed at conservation of avian species should balance restoration of early successional habitat with conservation of mature forest (Dettmers 2003, Artman et al. 2005, Bulluck and Buehler 2006, Buchler et al. 2007). Our results, and those of others (Artman et al. 2005, Greenberg et al. 2007), indicate conservation activities that foster avian diversity within the southern Appalachian Mountains may benefit from occasional high severity fires and a fire return interval of $3 \leq 10$ years. We are not suggesting all burns should be of high severity, only that the full range of fire severity be used through time and space.

Fire may be most beneficial to avian conservation when it is used over relatively large spatial scales (Artman et al. 2005, Greenberg et al. 2007). Managed fires will help develop a matrix of habitats and successional stages, and minimize the isolation of populations (Askins 2001, Brawn et al. 2001). A rationale against prescription of smaller-scale fires is that larger fires may be more easily controlled in habitat characterized by terrain similar to that in the Chattahoochee-Oconee National Forest. Larger burn units can make use of creeks and roads for fire breaks helping avoid undue disturbance such as plowing, which may be a vector for invasion of exotic species (Merriam et al. 2006). Our study did not examine the cumulative impacts of repeated low intensity burns, or combinations of burn intensities. However, our results suggest that medium and high intensity fires can have positive effects on bird communities and should be considered a valuable land management tool.

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AVIAN COMMUNITIES OF THE ALTAMAHA RIVER ESTUARY IN GEORGIA, USA

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ABSTRACT.—We surveyed male breeding birds in five habitats (bottomland forest, maritime oak [*Quercus* spp.], pine [*Pinus* spp.] forest, maritime shrub, saltmarsh) of coastal Georgia, USA using distance-sampling methods to estimate population densities. We examined species-habitat relationships using indicator species analysis (ISA). Acadian Flycatcher (*Empidonax virescens*) in bottomland forest, Northern Parula (*Parula americana*) in maritime oak, Brown-headed Nuthatch (*Sitta pusilla*) in pine forest, Clapper Rail (*Rallus longirostris*) in saltmarsh, and White-eyed Vireo (*Vireo griseus*) in shrub habitat ranked highest for Partners in Flight (PIF) priority species by densities. The ISA indicated fewer PIF priority species were associated with saltmarsh, but more species (6) were unique to saltmarsh than any other habitat. Indicator species occurred more often in maritime oak than bottomland forest (8 vs. 6), but both habitats had similar numbers of PIF priority species (4). Shrub habitat covered the smallest area (~0.2%) and had three PIF priority species, including Painted Bunting (*Passerina ciris*), the only PIF species with extremely high priority in this study. *Received 27 November 2009. Accepted 18 March 2010.*

Indicator species appeal to conservationists, land managers, and governmental agencies because they provide an efficient method of monitoring the impacts of environmental disturbances and management policies (Carignan and Villard 2002). Thus, indicator species analysis (ISA), based on combining frequency of occurrence and mean abundance (Dúfrêne and Legendre 1997), is gaining use in conservation studies (Graham and Blake 2001, Kirk and Hobson 2001, Morissette et al. 2002, Mouillot et al. 2002, Grundel and Pavlovic 2007). The use of indicator species can be helpful if it includes monitoring many species that represent different taxa and life histories, the chosen species monitored have excellent quantitative regional data, and habitat-related trends can be distinguished from natural variation (Carignan and Villard 2002).

Once a suite of indicator species has been chosen to represent a community, monitoring activities need to efficiently and reliably estimate appropriate population parameters that signal potential impacts to conservation stakeholders (Thomas 1996). Two relatively simple, yet meaningful, avian abundance parameter estimations for modeling population dynamics are species density and size (Buckland et al. 2001). Population size is the density times the area of appropriate habitat, and research has focused on improving estimates of population density. Other important parameters, including population demographics and survival, are more difficult to assess because they require capturing individuals (Nisbet 2001).

A common method used to estimate avian abundance has been count data (Hodges and Krementz 1996, Bajema et al. 2001, Rosenstock et al. 2002). The point-count method is relatively simple to conduct but assumes bird detection remains constant across different habitats, observer abilities, weather conditions, and species characteristics (Rosenstock et al. 2002). Distance-sampling methods yield more precise estimates of bird density than index methods, such as point counts, by adjusting for detection (Rosenstock et al. 2002, Thompson 2002). A 7-year comparison of point-count methods versus distance sampling found the latter method was more robust in large-scale, multispecies surveys (Norvell et al. 2003).

Distance-sampling methods have been used in many studies to assess quantitative differences in habitat use by avian species to distinguish species-habitat relationships (Hodges and Krementz 1996, Estades and Temple 1999, Fletcher and Koford 2002), but the method does not work well with rare species (Buckland et al. 2001). Conversely, ISA is valuable for assessing species-habitat correlations when species are rare, non-normality exists, where distance sampling may be logistically difficult, and where there may be no detection of a species at many sample sites (Mouillot et al. 2002).

Our objective was to examine avian communities and densities of male breeding bird species in

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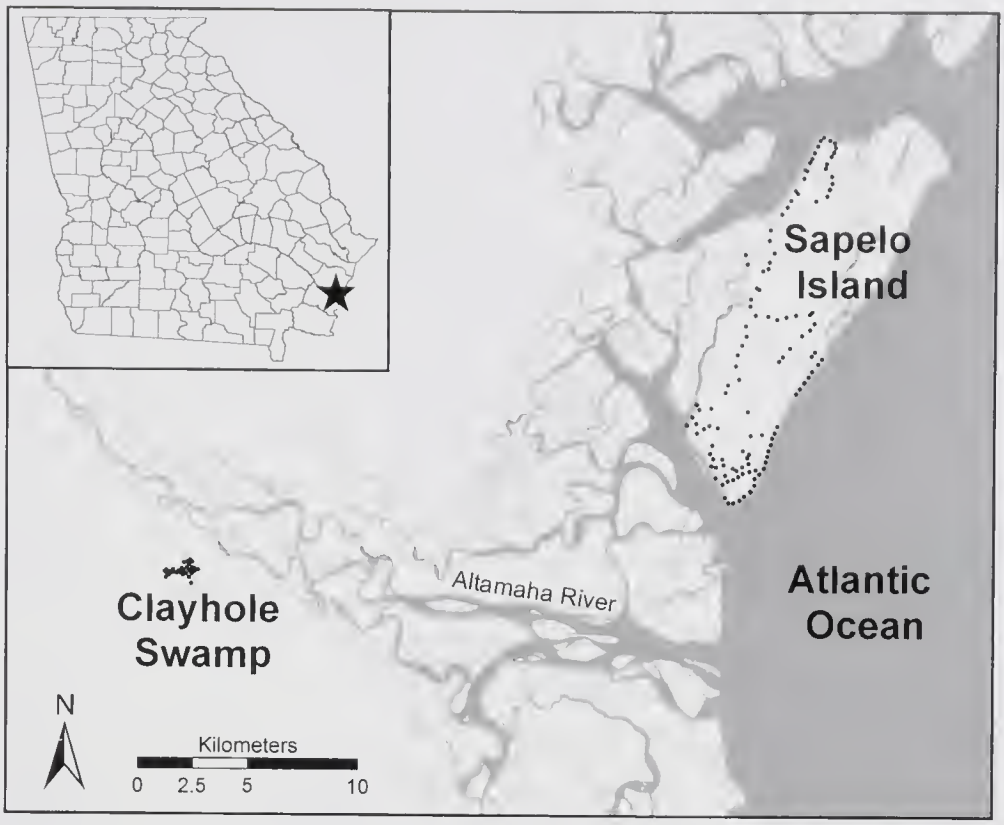

FIG. 1. Study area and sample sites on Sapelo Island, McIntosh County, Georgia and Clayhole Swamp, Glynn County, Georgia.

five habitats of coastal Georgia, USA (tidal-freshwater broadleaf deciduous forest, saltmarsh, maritime scrub-shrub, maritime broadleaf evergreen forest, and maritime narrowleaf evergreen forest).

METHODS

Study Area.—We surveyed broadleaf deciduous bottomland forest affected by tides, saltmarsh, maritime scrub-shrub, maritime broadleaf evergreen forest, and maritime narrowleaf evergreen forest in coastal Georgia, USA (Fig. 1) for male breeding birds. We selected a broadleaf deciduous forest affected by tides (bottomland forest) at the Clayhole Swamp Wildlife Management Area adjacent to the Altamaha River, Glynn County, Georgia, managed by the Department of Natural Resources (GDNR) (Duberstein and Kitchens 2007). We selected four other habitats on 6,677-ha Sapelo Island, McIntosh County, Georgia, managed by GDNR. We selected saltmarsh habitat primarily on the southwestern portions of the island and maritime scrub-shrub habitat (shrub) based on linear landscape features, such as secondary dunes, on the edge between forest and saltmarsh (Johnson et al. 1974). Maritime broadleaf evergreen forests (maritime oak [*Quercus* spp.]) were dominated by live oak (*Q. virginiana*), primarily on the north end of the island (Johnson et al. 1974). Maritime narrowleaf evergreen forests (pine [*Pinus* spp.] forest) consisted of loblolly pine (*P. taeda*) with scattered slash pine (*P. elliottii*) and were distributed throughout the island (Johnson et al. 1974). GDNR manages Sapelo Island's pine forests for sawtimber (old growth) using fire and timber harvest.

We selected bird sample points at least 250 m apart. We used a grid in bottomland forest starting from the southernmost accessible point via Honeygal Road. Saltmarsh sample points on Sapelo Island were randomly selected using a 1-m^2 grid overlain on a Geographic Information System (GIS) shapefile. Sample points in shrub habitat were in the ecotone between primary dunes and terrestrial forests on Sapelo Island. Oak and pine forest sample points were selected by driving one-lane sand roads and randomly locating them between 10 and 200 m on a line directly into forest patches that were relatively consistent within a 100-m radius.

Bird Sampling.—We conducted point counts following Ralph et al. (1993). We located 10 points in each habitat in 2006 (50 total) and an additional 20 points per habitat in 2007 (total of 150 points). Ten-minute counts were conducted twice at least 2 weeks apart at each point within 4 hrs of sunrise between 19 May and 9 June 2006, and between 17 May and 13 June 2007. The relative direction and distance of each detected bird from the sample point during each sampling event, excluding flyovers, were estimated. Distances were verified in the field on the way to the next point by pacing the distance from the point just sampled to a detected bird. Detections of the same species only included birds detected simultaneously or with obvious differences in plumage. Observer bias issues were limited by having a single observer conduct all sampling events.

Population Densities.—The density (# of birds/km^2) of species sampled using point counts was estimated in program DISTANCE 5.0 (Thomas et al. 2006) and equation $D = n/kv$, where D = density of birds per unit area, n = number of birds detected, k = number of points sampled, and v = the detection function of the species with distance from the sample point following Buckland et al. (2001). The detection function indicates the probability of detecting an individual as a function of distance from the sample points for a particular species (Buckland et al. 2001). The density of each species is calculated by fitting the frequency of detection as a function of distance into each of 12 theoretical models using the best fitting model (with the lowest Akaike's Information Criterion [AIC] value) (Buckland et al. 2001).

The frequency distribution of distance to detected (seen or heard) males for each species was pooled across all habitats to increase the sample size of detections. The cutoff for exclusion from DISTANCE analysis was <50 observations for a species across all habitats and <10 individuals of a species in a given habitat. We tested for differences in detection between habitat types using DISTANCE without pooling the frequency distribution across habitats, but only pooled results are presented due to lack of differences. Densities were considered to be different when there was a lack of overlap of the 95% confidence intervals (Gardner and Altman 1986, Hodges and Krementz 1996, Anderson et al. 2001, Fletcher and Koford 2002).

DISTANCE requires detection functions to monotonically decrease with distance from the sample point so the detection function is either flat or decreases with distance (Thomas et al. 2006). DISTANCE constrains parameters of the detection function at fixed points to fit the function to the model, if the detection function increases with distance. These constraints distort the detection function which may be better adjusted by truncating the tail of the data or altering the intervals to smooth the detection function (Thomas et al. 2006). We also conducted the analyses by truncating detections at 80- and 90-m, but only the non-truncated results are reported due to lack of differences. Models were chosen based on the least number of constrained parameters to obtain monotonicity and the lowest AIC value.

Statistics.—Species-habitat associations were assessed using indicator species analysis and 9999 Monte Carlo iterations (ISA; McCune and Grace 2002). ISA results include the relative abundance, relative frequency, highest indicator value, and P values of significant differences. Statistical results were considered significant at $\alpha < 0.05$. Dúfrêne and Legendre (1997) recommend a cutoff threshold indicator value (IV) of 25 for a species to be considered truly indicative of a habitat.

RESULTS

Species Abundance.—We detected 56 species during the two breeding seasons (scientific names and Partners in Flight priority status are in Table 1). We encountered Northern Cardinals and Carolina Wrens more often than any other species (401 and 400 encounters for 5 habitats, respectively). Red-eyed Vireos were most abundant in bottomland forest (142), Northern Parula in maritime oak (180), Red-bellied Woodpecker in pine forest (116), Clapper Rail in saltmarsh (150), and Northern Cardinal in shrub (140) (Table 2).

Bird Densities.—We estimated breeding male densities for 26 species overall (Table 2). None of the 14 species for which we estimated densities in bottomland forest was unique to this habitat, but Prothonotary Warbler and Barred Owl were only detected in bottomland forest. Tufted Titmouse densities were significantly higher in bottomland forest than all other species (172

TABLE 1. Species detected during point counts in five habitats in coastal Georgia during 2006 and 2007.

Species	Scientific name	AOU code
Great Blue Heron	*Ardea herodias*†	GBHE
Great Egret	*A. alba*†	GREG
Snowy Egret	*Egretta thula*†	SNEG
Yellow-crowned Night-Heron	*Nyctanassa violacea*†	YCNH
Red-shouldered Hawk	*Buteo lineatus*	RSHA
Red-tailed Hawk	*B. jamaicensis*	RTHA
Clapper Rail	*Rallus longirostris*†††	CLRA
Wilson's Plover	*Charadrius wilsonia*†††	WIPL
Willet	*Tringa semipalmata*††	WILL
Whimbrel	*Numenius phaeopus*	WHIM
Ruddy Turnstone	*Arenaria interpres*	RUTU
Mourning Dove	*Zenaida macroura*	MODO
Common Ground-Dove	*Columbina passerina*††	COGD
Yellow-billed Cuckoo	*Coccyzus americanus*††	YBCU
Barred Owl	*Strix varia*	BADO
Ruby-throated Hummingbird	*Archilochus colubris*	RTHU
Red-headed Woodpecker	*Melanerpes erythrocephalus*††	RHWO
Red-bellied Woodpecker	*M. carolinus*	RBWO
Downy Woodpecker	*Picoides pubescens*	DOWO
Pileated Woodpecker	*Dryocopus pileatus*	PIWO
Eastern Wood-Pewee	*Contopus virens*†	EAWP
Acadian Flycatcher	*Empidonax virescens*†	ACFL
Great Crested Flycatcher	*Myiarchus crinitus*	GCFL
Eastern Kingbird	*Tyrannus tyrannus*	EAKI
White-eyed Vireo	*Vireo griseus*††	WEVI
Yellow-throated Vireo	*V. flavifrons*†	YTVI
Red-eyed Vireo	*V. olivaceus*	REVI
Blue Jay	*Cyanocitta cristata*	BLJA
American Crow	*Corvus brachyrhynchos*	AMCR
Fish Crow	*C. ossifragus*	FICR
Carolina Chickadee	*Poecile carolinensis*††	CACH
Tufted Titmouse	*Baeolophus bicolor*	TUTI
Brown-headed Nuthatch	*Sitta pusilla*†††	BHNU
Carolina Wren	*Thryothorus ludovicianus*	CARW
Marsh Wren	*Cistothorus palustris*	MAWR
Blue-gray Gnatcatcher	*Polioptila caerulea*	BGGN
Eastern Bluebird	*Sialia sialis*	EABL
Northern Mockingbird	*Mimus polyglottos*	NOMO
Brown Thrasher	*Toxostoma rufum*	BRTH
Northern Parula	*Parula americana*†††	NOPA
Yellow-throated Warbler	*Dendroica dominica*†††	YTWA
Pine Warbler	*D. pinus*††	PIWA
Prothonotary Warbler	*Protonotaria citrea*††	PROW
Common Yellowthroat	*Geothlypis trichas*	COYE
Hooded Warbler	*Wilsonia citrina*†††	HOWA
Yellow-breasted Chat	*Icteria virens*†	YBCH
Eastern Towhee	*Pipilo erythrophthalmus*††	EATO
Seaside Sparrow	*Ammodramus maritimus*†††	SESP
Summer Tanager	*Piranga rubra*†	SUTA
Northern Cardinal	*Cardinalis cardinalis*	NOCA
Blue Grosbeak	*Passerina caerulea*	BLGR
Painted Bunting	*P. ciris*††††	PABU
Red-winged Blackbird	*Agelaius phoeniceus*	RWBL
Boat-tailed Grackle	*Quiscalus major*	BTGR
Brown-headed Cowbird	*Molothrus ater*	BHCO
Orchard Oriole	*Icterus spurius*††	OROR

† Local interest species (Hunter et al. 2001).
†† Moderate priority species.
††† High priority species.
†††† Extremely high priority species.

TABLE 2. Total detections (counts) and breeding male population densities (birds/km^2) with 95% confidence interval (in parentheses) calculated using DISTANCE for birds breeding in five habitats of coastal Georgia.

Species	Bottomland forest		Maritime oak		Pine forest		Saltmarsh		Shrub	
	Count	Density (CI)	Count	Density (CI)	Count	Density (CI)	Count	Density (CI)	Count	Density (CI)
Great Blue Heron					1		4			
Great Egret							14			
Snowy Egret							2			
Yellow-crowned Night-Heron	6		2				1			
Clapper Rail							150	98 (58–163)		
Red-shouldered Hawk	9				1					
Red-tailed Hawk			3		4					
Wilson's Plover							9		2	
Whimbrel							7			
Willet							9		2	
Ruddy Turnstone							9			
Mourning Dove	2		7		26				9	
Common Ground-Dove									5	
Yellow-billed Cuckoo	30		1		1				1	
Barred Owl	5									
Ruby-throated Hummingbird	2		3		3				3	
Red-headed Woodpecker			6		19				2	
Red-bellied Woodpecker*	79	62 (55–71)[a]	88	72 (63–82)[a,b]	116	91 (79–104)[b]			12	8 (7–9)[c]
Downy Woodpecker	18	32 (13–67)	27	49 (23–101)	23	41 (20–86)			14	25 (12–52)
Pileated Woodpecker*	32	18 (12–26)	18	10 (6–16)	13	8 (4–14)			2	
Eastern Wood-Pewee*	1		37	19 (17–22)	41	21 (19–24)				
Acadian Flycatcher	53	112 (83–152)[a]	42	89 (62–127)[a]	16	34 (19–59)[b]				
Great Crested Flycatcher*	26	31 (27–36)[a]	78	93 (79–108)[b]	63	75 (64–87)[b]			19	20 (18–24)[c]
Eastern Kingbird					1		20		3	
White-eyed Vireo*	17	21 (19–24)[a]	140	172 (151–195)[b]	101	123 (109–139)[c]			99	121 (107–136)[c]
Yellow-throated Vireo*	2		33	29 (20–43)	22	19 (12–32)			1	
Red-eyed Vireo*	142	125 (106–148)[a]	19	17 (11–28)[b]	10	9 (5–18)[b]			1	
Blue Jay	12		10		18				3	
American Crow	7		10		13				4	
Fish Crow			16		8				4	
Carolina Chickadee	29	79 (54–115)	45	120 (83–173)	40	104 (72–149)			31	74 (51–106)
Tufted Titmouse	86	172 (138–214)	70	147 (114–188)	52	108 (78–151)			6	
Brown-headed Nuthatch			11	51 (43–62)[a]	66	299 (248–359)[b]			9	
Carolina Wren	109	94 (85–104)[a]	119	103 (93–115)[a]	99	88 (79–97)[a]			73	64 (58–70)[b]

TABLE 2. Continued.

Species	Bottomland forest		Maritime oak		Pine forest		Saltmarsh		Shrub	
	Count	Density (CI)	Count	Density (CI)	Count	Density (CI)	Count	Density (CI)	Count	Density (CI)
Marsh Wren							73	65 (34–126)		
Blue-gray Gnatcatcher	20	149 (100–222)[a]	51	346 (233–515)[b]	50	346 (233–515)[b]			51	319 (214–475)[a,b]
Eastern Bluebird					13					
Northern Mockingbird					2				5	
Brown Thrasher					5				3	
Northern Parula	65	91 (87–95)[a]	180	251 (232–271)[b]	63	87 (82–92)[a]			11	10 (9–10)[c]
Yellow-throated Warbler*			121	119 (101–140)[a]	91	93 (79–109)[a]			16	17 (14–20)[b]
Pine Warbler			39	55 (46–65)[a]	88	122 (102–146)[b]			36	48 (40–57)[a]
Prothonotary Warbler	23									
Common Yellowthroat			4		19				5	
Hooded Warbler	38		4							
Yellow-breasted Chat					10				34	
Eastern Towhee			8		41	55 (38–80)[a]			83	113 (87–148)[b]
Seaside Sparrow							14			
Summer Tanager	33	35 (28–45)[a]	30	35 (28–45)[a]	26	30 (24–37)[a]			15	17 (14–22)[b]
Northern Cardinal	68	85 (76–94)[a]	82	99 (89–109)[a]	111	133 (119–148)[b]			140	170 (152–190)[c]
Blue Grosbeak					6				12	
Painted Bunting*			10	15 (11–19)[a]	17	21 (16–27)[a]			67	80 (62–104)[b]
Red-winged Blackbird*							148	125 (71–220)[a]	37	30 (15–58)[b]
Boat-tailed Grackle							86	69 (43–109)	11	18 (5–61)
Brown-headed Cowbird	2		13	28 (14–55)	22	47 (28–80)			21	26 (15–45)
Orchard Oriole			1		2				13	

* Species whose density models had parameters constrained to obtain monotonicity.
[a,b,c] Groups of population densities with overlapping confidence intervals for each species among habitats.

TABLE 3. Model type, goodness of fit (GOF), *P*-value of GOF, coefficient of variation (CV) and degrees of freedom (df) for selected DISTANCE models. "hn" = half-normal key function, "hr" = hazard rate key function, "ne" = negative exponential key function, and "un" = uniform key function. "cos" = cosine series expansion, "sp" = simple polynomial series expansion, and "hp" = hermite polynomial series expansion.

Habitat	Species	Model	GOF D_n	*P*-value	CV	df
Maritime oak	Red-bellied Woodpecker	hr+cos	0.1448	0.0001	6.70	307.92
	Downy Woodpecker	ne+hp	0.1685	0.0190	38.08	80.18
	Pileated Woodpecker	hr+cos	0.1282	0.2284	23.49	34.28
	Eastern Wood-Pewee	hr+cos	0.1437	0.0764	6.37	82.75
	Acadian Flycatcher	hn+sp	0.1107	0.1318	17.91	70.84
	Great Crested Flycatcher	hr+cos	0.1288	0.0048	7.81	200.44
	White-eyed Vireo	hr+cos	0.0664	0.0908	6.46	256.53
	Yellow-throated Vireo	hr+cos	0.1691	0.0726	19.33	67.18
	Red-eyed Vireo	hr+cos	0.1136	0.0268	24.47	31.77
	Carolina Chickadee	hr+cos	0.0798	0.3429	18.79	140.03
	Tufted Titmouse	hn+sp	0.1186	0.0059	12.49	71.31
	Brown-headed Nuthatch	hn+cos	0.1210	0.1762	9.31	84.68
	Carolina Wren	hr+sp	0.0817	0.0104	5.36	295.43
	Blue-gray Gnatcatcher	ne+sp	0.0967	0.0816	20.35	167.47
	Northern Parula	un+cos	0.1504	0.0001	3.78	33.95
	Yellow-throated Warbler	hr+cos	0.0729	0.1975	8.28	244.66
	Pine Warbler	hn+sp	0.1438	0.0027	9.10	172.12
	Summer Tanager	hr+sp	0.0589	0.8676	11.54	107.99
	Northern Cardinal	hr+sp	0.0694	0.0444	5.26	375.20
	Painted Bunting	hn+sp	0.1611	0.0124	13.11	101.90
	Brown-headed Cowbird	hn+sp	0.1543	0.1937	34.54	43.19
Pine forest	Red-bellied Woodpecker	hr+cos	0.1448	0.0001	6.81	305.86
	Downy Woodpecker	ne+hp	0.1685	0.0190	38.10	80.34
	Pileated Woodpecker	hr+cos	0.1282	0.2284	29.95	32.12
	Eastern Wood-Pewee	hr+cos	0.1437	0.0764	6.43	85.46
	Acadian Flycatcher	hn+sp	0.1107	0.1318	28.37	40.39
	Great Crested Flycatcher	hr+cos	0.1288	0.0048	7.73	195.61
	White-eyed Vireo	hr+cos	0.0664	0.0908	6.15	324.93
	Yellow-throated Vireo	hr+cos	0.1691	0.0726	25.23	48.09
	Red-eyed Vireo	hr+cos	0.1136	0.0268	33.62	30.42
	Carolina Chickadee	hr+cos	0.0798	0.3429	18.72	137.96
	Tufted Titmouse	hn+sp	0.1186	0.0059	16.54	46.64
	Brown-headed Nuthatch	hn+cos	0.1210	0.1762	9.34	85.73
	Carolina Wren	hr+sp	0.0817	0.0104	5.21	343.74
	Blue-gray Gnatcatcher	ne+sp	0.0967	0.0816	20.36	167.50
	Northern Parula	un+cos	0.1504	0.0001	2.59	41.23
	Yellow-throated Warbler	hr+cos	0.0729	0.1975	8.18	242.31
	Pine Warbler	hn+sp	0.1438	0.0027	9.20	177.27
	Eastern Towhee	hn+sp	0.1553	0.0038	18.59	32.23
	Summer Tanager	hr+sp	0.0589	0.8676	11.43	104.20
	Northern Cardinal	hr+sp	0.0694	0.0444	5.54	290.03
	Painted Bunting	hn+sp	0.1611	0.0124	13.15	102.91
	Brown-headed Cowbird	hn+sp	0.1543	0.1937	26.72	55.86
Saltmarsh	Clapper Rail	ne+sp	0.1060	0.0704	26.39	123.74
	Marsh Wren	hn+sp	0.1050	0.3962	33.63	46.69
	Red-winged Blackbird	nc+sp	0.1285	0.0040	29.21	195.84
	Boat-tailed Grackle	hn+sp	0.1874	0.0010	23.32	62.01

TABLE 3. Continued.

Habitat	Species	Model	GOF D_n	*P*-value	CV	df
Shrub	Red-bellied Woodpecker	hr+cos	0.1448	0.0001	6.76	308.85
	Downy Woodpecker	ne+hp	0.1685	0.0190	38.09	80.23
	Great Crested Flycatcher	hr+cos	0.1288	0.0048	7.89	204.97
	White-eyed Vireo	hr+cos	0.0664	0.0908	6.26	305.61
	Carolina Chickadee	hr+cos	0.0798	0.3429	18.82	140.79
	Carolina Wren	hr+sp	0.0817	0.0104	5.02	403.37
	Blue-gray Gnatcatcher	ne+sp	0.0967	0.0816	20.37	168.12
	Northern Parula	un+cos	0.1504	0.0001	1.98	56.49
	Yellow-throated Warbler	hr+cos	0.0729	0.1975	8.08	238.23
	Pine Warbler	hn+sp	0.1438	0.0027	9.13	174.24
	Eastern Towhee	hn+sp	0.1553	0.0038	13.24	37.09
	Summer Tanager	hr+sp	0.0589	0.8676	11.44	104.52
	Northern Cardinal	hr+sp	0.0694	0.0444	5.61	274.44
	Painted Bunting	hn+sp	0.1611	0.0124	13.15	102.81
	Red-winged Blackbird	ne+sp	0.1285	0.0040	34.25	119.98
	Boat-tailed Grackle	hn+sp	0.1874	0.0010	67.34	32.58
	Brown-headed Cowbird	hn+sp	0.1543	0.1937	27.90	54.75
Bottomland forest	Red-bellied Woodpecker	hr+cos	0.1448	0.0001	6.73	307.94
	Downy Woodpecker	ne+hp	0.1685	0.0190	38.08	80.20
	Pileated Woodpecker	hr+cos	0.1282	0.2284	20.35	36.29
	Acadian Flycatcher	hn+sp	0.1107	0.1318	15.26	100.71
	Great Crested Flycatcher	hr+cos	0.1288	0.0048	7.68	192.55
	White-eyed Vireo	hr+cos	0.0664	0.0908	6.15	325.09
	Red-eyed Vireo	hr+cos	0.1136	0.0268	8.33	71.85
	Carolina Chickadee	hr+cos	0.0798	0.3429	19.16	149.10
	Tufted Titmouse	hn+sp	0.1186	0.0059	11.09	95.60
	Carolina Wren	hr+sp	0.0817	0.0104	5.15	363.55
	Blue-gray Gnatcatcher	ne+sp	0.0967	0.0816	20.38	168.33
	Northern Parula	un+cos	0.1504	0.0001	2.14	49.57
	Summer Tanager	hr+sp	0.0589	0.8676	11.48	105.93
	Northern Cardinal	hr+sp	0.0694	0.0444	5.38	339.58

males/km^2). Red-eyed Vireo densities were significantly higher in bottomland forest than any other habitat. We estimated breeding male densities for four species in saltmarsh, but seven species were unique to saltmarsh (Table 2). Red-winged Blackbirds had significantly higher densities in saltmarsh than all other habitats, and had the highest density of any saltmarsh species (125 males/km^2).

We estimated densities of breeding males for 17 species in shrub habitat (Table 2). None of these species was unique to this habitat, but Common Ground-Doves were only detected in shrublands. Eastern Towhee, Northern Cardinal, and Painted Bunting males had significantly higher densities in shrub than other habitats. We estimated male densities for 21 species in maritime oak and 22 species in pine forest, but none of these species was unique to either habitat, although Eastern Bluebirds were only detected in pine forest. Northern Parula and White-eyed Vireo had significantly higher densities in maritime oak than other habitats. Brown-headed Nuthatch and Pine Warbler had significantly higher densities in pine forest than other habitats. The highest estimated density in shrub, maritime oak, and pine forest was for Blue-gray Gnatcatcher (319, 346, and 346 males/km^2, respectively).

Most DISTANCE models used either the half-normal key function with a simple polynomial series expansion (31%) or the hazard-rate key function with a cosine series expansion (35%) (Table 3). The *P*-values for the Kolmogorov-Smirnov Goodness of Fit tests of each model were <0.10 for 17 of the 26 species (65%).

Indicator Species Analysis.—We calculated that 28 species were indicators of one of the five habitats in coastal Georgia using Dufrêne

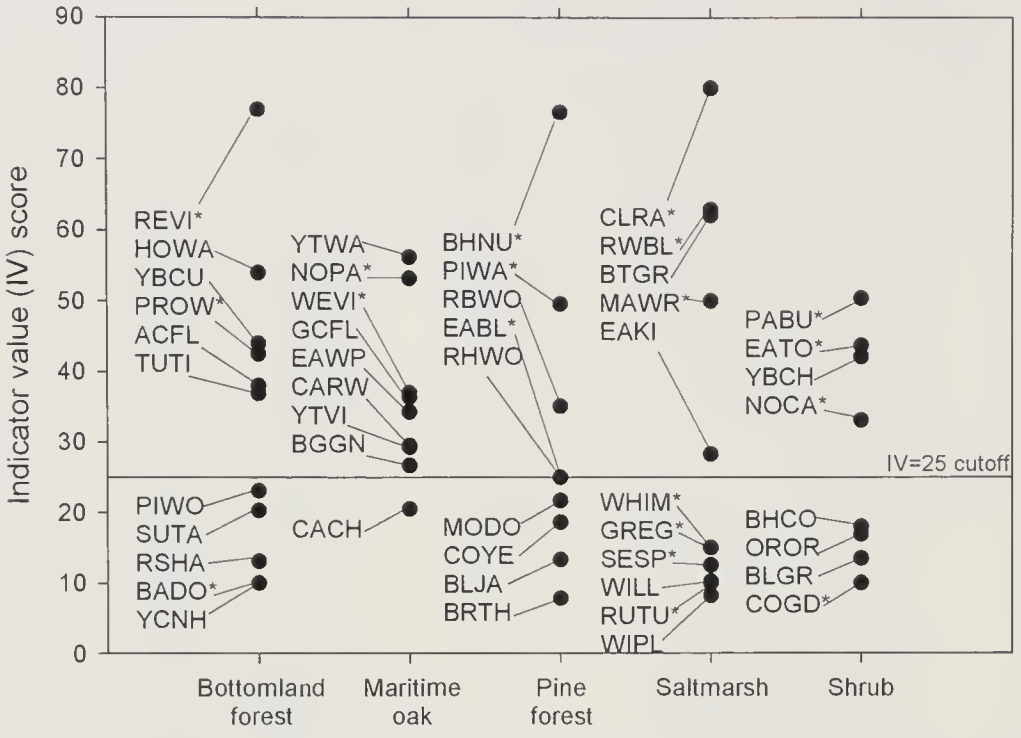

FIG. 2. Indicator Value (IV) scores for species in each of five habitats in coastal Georgia, USA. Also shown is the indicator cutoff value (25) of Dúfrêne and Legendre (1997). * = species unique to the habitat or that have higher densities in the habitat in distance sampling.

and Legendre's (1997) IV > 25 cutoff; an additional 21 species were indicators according to the ISA but had IV scores < 25 (Fig. 2). Six species were indicative of bottomland forest and five species were indicative of saltmarsh. Shrub habitat had the fewest indicator species (4), but the species with the highest IV score in shrub habitat was the only extremely high priority species in the region, Painted Bunting. Eight species were indicators of maritime oak and five were indicators of pine forest.

DISCUSSION

Implications for Conservation.—We estimated a proportionately high number of PIF priority species were indicative of bottomland forest (4), which occupies ~10.0% of the coastal Georgia landscape (Brittain 2009). Prothonotary Warblers occurred in bottomland forest sites with high forest cover and basal area along tidal channels (Petit 1999). Similarly, Acadian Flycatchers and Yellow-billed Cuckoos were indicative of wetland forests typical of their southeastern habitats (Stevenson and Anderson 1994, Whitehead and Taylor 2002); Acadian Flycatchers were also abundant in maritime oak. Yellow-throated Warblers may have been deterred from occupying bottomland forests, despite another study that observed them in that habitat type (Hall 1996), by the absence of large dead trees (Hamel 1992).

Georgia saltmarshes had the lowest number of priority indicator species among the habitats studied (1), but the highest diversity of species unique to the habitat. Seaside Sparrows occurred exclusively in tall smooth cordgrass (*Spartina alterniflora*) stands on the banks of larger estuaries with extensive mudflats (Post and Greenlaw 1994). Clapper Rails were detected in tall *Spartina* of the low marsh and the shrubby vegetation in the high marsh-upland ecotone (Eddleman and Conway 1998). Tall *Spartina* may be important as habitat for Seaside Sparrows and other saltmarsh birds, such as Marsh Wrens, by creating areas of dense vegetation for secure nests.

Eastern Towhees and Yellow-breasted Chats in coastal Georgia, both PIF priority species, were more abundant in shrub habitat than in open forest (Greenlaw 1996, Eckerle and Thompson 2001). Common Ground-Doves were found only in coastal dunes despite known use of open pine, hummocks, and forest edges (Bowman 2002) common on Sapelo Island, likely due to the lack of bare soil in forest habitats (Hamel 1992). The PIF Conservation Plan defines quality shrub

habitat as "largely forested areas with some edge and forest openings for buntings" (Hunter et al. 2001). However, shrub habitat, where Painted Buntings, Eastern Towhees, and Yellow-breasted Chats were far more common in this and another study (Springborn and Meyers 2005), was largely composed of coastal dunes. Maritime scrub-shrub habitat deserves conservation priority over other habitats as it occupies only ~0.2% of the coastal Georgia landscape (Brittain 2009) and is important for the area's only species of extremely high conservation priority.

Northern Parula occupied mature hardwood forests with Spanish moss (*Tillandsia usneoides*) (maritime oak type) and floodplains with blue palm (*Brahea armata*) (bottomland forest type), as reported by Moldenhauer and Regelski (1996), but were far more abundant in maritime oak. Similarly, Eastern Wood-Pewee and Yellow-throated Vireo occurred in all three forest types, but were more common in maritime oak (McCarty 1996, Rodewald and James 1996). The ISA also revealed White-eyed Vireos were indicators of maritime oak rather than the shrub habitat for which they are listed by PIF (Hunter et al. 2001).

A PIF Conservation Plan goal in pine forest includes emphasis on late successional stands with increasing disturbance regimes to enhance understory habitat quality (Hunter et al. 2001). Managed disturbances, such as prescribed fire and logging on Sapelo Island, maintain the open stands of mature pine habitat preferred by Brown-headed Nuthatches (Withgott and Smith 1998). However, this conservation plan may aid Brown-headed Nuthatches and Red-headed Woodpeckers but may harm Pine Warbler populations dependent on a well-developed shrub layer (Rodewald et al. 1999, Smith et al. 2000). Pine forest occupies nearly half of the coastal Georgia landscape (Brittain 2009), and there may be opportunity for diverse strategies to protect associated species.

Bird Densities.—Assumptions in distance sampling include complete detection of all individuals close to the sample point and that birds do not leave the sampling area prior to detection (Buckland et al. 1993, Thompson 2002). The detection rates in our study generally increased within the first 5–10 m of the sample point before declining, indicating birds may have moved from the sample point as the observer approached, or the area of near-perfect detection extended ~5 m beyond the sample point itself.

DISTANCE could not find acceptable detection functions without constraining parameters to obtain monotonicity for 10 species (38%). Constraining the parameters may have distorted the detection functions and skewed the results. However, alternative methods, such as truncation, did not resolve the constrained parameter issues and yielded results that were not significantly different than those calculated using the original data. The lack of good fit for 65% of the detection functions increased concerns about the model results, but truncation and grouping the data into intervals made the fit worse, as reflected by lower *P*-values in the Kolmogorov-Smirnov tests, and did not significantly change the results.

Forest structure may hamper detection of silent and sedentary individuals, whereas open habitats, such as saltmarsh, should allow for near complete detection (Pacifici et al. 2008). Thus, breeding male density estimates in forested habitats were likely underestimated. Detection variations among different habitats should be considered (Simons et al. 2007) by limiting the pooling of data to create the detection functions. However, we believed increased sample size outweighed detection differences between habitats. We tested each species without pooling the detection frequency data and the results showed no significant differences between pooled and non-pooled data for most species (not presented). The 95% confidence intervals for each of the species were significantly lower in the non-pooled data than pooled data for White-eyed Vireo (maritime oak and pine forest), Blue-gray Gnatcatcher (shrub), and Yellow-throated Warbler (shrub). Yellow-throated Warblers also had a significantly higher density estimate for maritime oak using the non-pooled data. However, all models had to constrain parameters to obtain monotonicity using non-pooled frequency data, and had lower Goodness of Fit *P*-values, indicating these models were less reliable than those using the pooled data. The lack of improved models and differences in density estimates between results using pooled versus non-pooled frequency data led us to conclude the pooled data were safer to use.

Some breeding male densities appear high, particularly Blue-gray Gnatcatchers, Brown-headed Nuthatches in pine forest, Northern Parula in maritime oak, and White-eyed Vireos on Sapelo

Island. Male Brown-headed Nuthatches, found almost exclusively in pine forests, were often observed traveling in family groups that may have skewed results by being more easily detected in family clusters than individually. Northern Parulas were definitively more abundant in maritime oak and the number of males captured during bird banding attempts was similar to the number of detected males (Brittain 2009). White-eyed Vireos and Blue-gray Gnatcatchers appeared curious about the observer's presence at the sample point, which may have positively biased estimated densities.

Our measurements of densities of six species (Acadian Flycatcher, Blue-gray Gnatcatcher, Northern Parula, Prothonotary Warbler, Red-eyed Vireo, White-eyed Vireo) were greater than those reported by Hodges and Krementz (1996). These differences may be the result of variations in study design or individual bird detection skills. Northern Parula densities in upstream riparian corridors were similar to densities in shrub habitat in this study (Hodges and Krementz 1996).

Distance sampling indicated the PIF priority species with the highest densities were: Acadian Flycatcher in bottomland forest, Northern Parula in maritime oak, Brown-headed Nuthatch in pine forest, Clapper Rail in saltmarsh, and White-eyed Vireo in shrub habitat. Shrub habitat should have the highest conservation value since it had the highest proportion of indicator species that were also PIF priority species (75%), the only extremely high priority indicator species (Painted Bunting), and occupied a much smaller portion of the coastal landscape (~0.2%) than other habitats. Maritime oak, bottomland forests, and saltmarsh cover moderate portions of coastal Georgia, but forest habitats had more PIF priority indicator species than saltmarsh (5, 4, and 1, respectively). Protections given tidal wetlands under Section 404 of the Clean Water Act (e.g., bottomland forest and saltmarsh; PL 92-500, 33 USC 1251), combined with the high percentage of priority species, suggests avian conservation efforts should focus on conserving maritime oak habitat. Pine forest is relatively plentiful and was equal to shrub for the least number of PIF priority indicator species in upland habitat.

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INFLUENCE OF COVER AND FOOD RESOURCE VARIATION ON POST-BREEDING BIRD USE OF TIMBER HARVESTS WITH RESIDUAL CANOPY TREES

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ABSTRACT.—We investigated avian use of clearcuts and two-age harvests during the post-breeding period in 2006 in the central Appalachians, West Virginia, USA with an information-theoretic approach to model selection. Cover variables appeared to be most important; e.g., vegetative vertical complexity had a strong positive relation with capture rates of mature forest birds and molting adults, as well as physical condition which supports a predator-avoidance hypothesis for habitat use. Basal area was a poor predictor of captures; residual trees near nets tended to depress capture rates. Food variables best explained capture rates for some species groups (e.g., early-successional insectivores and granivores, mature forest nesting adults, molting birds), but post-breeding habitat quality was based primarily on vegetative cover. Habitat use may depend on the bird's physical condition and molt status, and we found evidence for age-specific differences which may impact survival. Our study suggests important links between post-breeding habitat quality, molt status, physical condition, and bird age, and indicates a variety of response variables (relative abundance, survival, body condition) should be measured to assess avian habitat quality during the post-breeding period. *Received 19 March 2009. Accepted 6 February 2010.*

Recent declines in populations of migratory birds that nest in both mature forest and early-successional habitats have stimulated interest in limiting factors and potential mortality sources throughout the year (Robbins et al. 1989, Hunter et al. 2001). Habitat loss and fragmentation in breeding and wintering areas are probable factors (Askins et al. 1990), but little is known about factors affecting survival during the post-breeding period (Baker 1993, Pagen et al. 2000), the interval between fledging of young and migration. Many bird species that nest in early-successional or mature forest habitats use early-successional habitat extensively during post-breeding. For example, many species of mature forest breeding songbirds move into nearby shrublands after young have fledged (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2007). Juvenile Wood Thrush (*Hylocichla mustelina*) and Swainson's Thrush (*Catharus ustulatus*) are also known to move >1 km from their mature forest natal area into early-successional habitat before migration (Anders et al. 1998, Vega Rivera et al. 1998, White et al. 2005, Dellinger 2007).

One explanation for this behavior is predator avoidance; early-successional habitats may provide increased protection from predators (White et al. 2005). A dense understory provides cover for fledglings that, lacking the knowledge to detect and escape predators, often have high post-fledging mortality (Sullivan 1989, Anders et al. 1997). Adults may also seek protection and cover during the post-breeding period as they undergo pre-basic molt and are temporarily more vulnerable to predators (Pagen et al. 2000). More understory vegetation and increased vertical structure were associated with increased survival for fledgling Ovenbirds (*Seiurus aurocapilla*) (Vitz 2008), even where prey abundance was low (King et al. 2006).

A second explanation is the resource-selection, or optimal-foraging hypothesis (i.e., bird use of early-successional habitats is driven by greater food resource abundance) (White et al. 2005). Abundant food resources are needed by both adults and juveniles for accumulation of fat reserves in preparation for migration and completion of molt (Murphy and King 1992, DeGraaf and Yamasaki 2003). Molt is nutritionally demanding and requires energy and protein not only for synthesizing feathers, but for increasing metabolism to offset reduced insulation and flight efficiency (Jenni and Winkler 1994). Juvenile Swainson's Thrush use of coastal scrub during post-fledging was best explained by fruit abundance variables, supporting the resource-selection hypothesis (White et al. 2005).

Two-age harvesting or green-tree retention, where canopy trees are retained to more closely resemble natural disturbances, is becoming more common (Franklin et al. 1997, Rose and Muir

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1997, Vanha-Majamaa and Jalonen 2001, Vergara and Schlatter 2006), and is frequently used as an alternative to clearcut harvests in central Appalachian hardwood forests (Miller et al. 2006). Mature residual trees and a regenerating age class provide vertical stratification for both shrub and canopy-associated birds (Duguay et al. 2000). The effects of two-age harvesting on breeding birds have been demonstrated (Baker and Lacki 1997, Boardman and Yahner 1999, Duguay et al. 2000, McDermott and Wood 2009), but no studies of which we are aware have examined avian use of stands with residual tree retention during the post-breeding period.

The objectives of this study were to: (1) quantify how vegetative structure and food availability in timber harvests with a gradient of residual canopy trees affect post-breeding bird habitat use, and (2) examine the impacts of resource variation on avian body condition and molt status. Our study is unique in that we examine both mature forest and early-successional nesting bird species, investigate multiple types of food resources at the nest-level, and integrate molt and body condition variables.

METHODS

Study Areas.—Our study was conducted in West Virginia on the Monongahela National Forest (MNF) in Pocahontas and Tucker counties (38° 31′ N, 79° 44′ W), and the Wildlife and Ecosystem Research Forest (WERF) in Randolph County (38° 43′ N, 80° 03′ W). These managed forests in the central Appalachian Mountains are characterized by narrow, low valleys dissected by northeast-southwest ridges.

We selected nine stands with a gradient of retained basal area ranging from 0 to 7 m^2/ha for sampling. Stand age (4–7 years post-harvest) was a selection criterion, because there were few harvests in an early-successional stage. We chose stands on the MNF (n = 5) that were in close proximity to those on the WERF (n = 4). Harvest area was 4.2–21 ha and elevation was 630–1,090 m.

The principal forest types were northern Allegheny hardwoods, cove hardwoods, mixed mesophytic, and oak-hickory (*Quercus* spp.-*Carya* spp.). Dominant overstory tree species included red oak (*Q. rubra*), red maple (*Acer rubrum*), chestnut oak (*Q. prinus*), and yellow poplar (*Liriodendron tulipifera*). The most abundant understory plants were blackberry (*Rubus* spp.), black birch (*Betula lenta*), greenbrier (*Smilax* spp.), American beech (*Fagus grandifolia*), maples, and yellow poplar.

Mist-Netting.—We used mist nets to sample bird habitat use because surveying birds by vision is difficult in dense vegetation, and many birds are secretive during the post-breeding period (Ralph et al. 2004). Our goal was to relate bird capture rates to microhabitat food and cover variables. We placed 10 mist nets (12 × 2.6 m with 30 mm mesh) in each stand, often along skid roads created during timber harvest and usually oriented perpendicular to the prevailing aspect. We arranged nets so that distance from edge was variable; a minimum of 20 m separated ends of nets, and each net was within 60 m of another net. We first sampled stands randomly and conducted repeat visits in the same order at least 3 weeks apart. A stand (n = 3) from each harvest type (clearcut, low-leave two-age, and high-leave two-age) was randomly chosen for the first round, and alternated for each sampling round.

We sampled 2 consecutive days at each stand and visited each twice from 25 June to 15 August 2006. We opened nets at sunrise and closed after 4–5 hrs except in inclement weather, when mist nets were not operated. We checked nets every 30 min and recorded species, age, gender, wing chord, mass, fat, breeding condition (extent of brood patch or cloacal protuberance), molt status, and time of capture for each captured individual. Captured birds, except for Ruby-throated Hummingbirds (*Archilochus colubris*), were fitted with USGS aluminum bands. We filled out molt cards per the British Trust for Ornithology for actively molting adults to obtain pre-basic molt scores.

Food Resource Sampling.—We sampled fruits twice in each stand, once per round immediately after the first day of mist-netting. We obtained an index of fruit abundance by counting individual fruits along 12-m transects within 1 m of either side of each mist-net lane (Levey 1988). All fruits were counted, identified to species, and classified as unripe or ripe.

We also collected arthropod samples, concurrently with fruit sampling, to obtain biomass availability estimates (Hutto 1990, Smith and Rotenberry 1990). We used biomass as an index of food availability, not an absolute measure of food consumed by birds (Hutto 1990, Duguay et al. 2000). We obtained four arthropod samples at each net location (n = 90), one from each of four saplings, each round. Saplings within 10 m of the

nets were beaten with a rubber mallet to dislodge arthropods (Schauff 1997). This capture method was most suitable for sampling arthropods available to foliage-gleaning birds, the most common foraging guild captured in the pilot year (McDermott 2007). Samples were taken from two random tree saplings within mist-net height on each side of the net. We often used the same individual trees in the second round, as the time interval (~3 weeks) allowed sufficient time for repopulation (Linda Butler, Entomologist, West Virginia University, pers. comm.).

We used a sturdy, light-colored sheet, 1 m^2 in area to capture the arthropods. The sheet was held under the branches of one side of the sapling, and one person beat four limbs that were above the sheet from top to bottom (four beats per limb). Once specimens fell onto the sheet, small arthropods were collected with an aspirator into a glass vial of ethanol. We picked up larger insects with forceps and placed them into a vial. Specimens were stored in 70% ethanol.

We identified all arthropods to Order, and classified each individual into one of three size categories: <3, 3–10, and >10 mm (Van Horne and Bader 1990). Specimens were subsequently placed on a tray and inserted into a drying oven at 60° C. We weighed each sample (by taxonomic Order, size, net, and round) to the nearest 0.1 mg to obtain an estimate of biomass after 48 hrs or when specimens achieved a constant mass. Arthropod richness at the Order level was calculated as a measure of arthropod diversity.

Vegetation Sampling.—We recorded presence or absence of vegetative cover on four 12-m transects, 3 m and 6 m from the net paralleling each side of the net lane (Schemske and Brokaw 1981), at five equidistant intervals along each transect in height categories: 0–1 , >1–2 , >2–3 , >3–6 , >6–12 , >12–18 , >18–24 , and >24 m. A vertical complexity index (VCI) was calculated as a sum of all height cover class percentages divided by 100 and multiplied by a constant (Wood et al. 2005). We quantified the number of stems <7.6 cm dbh and percent ground cover categorized as leaf litter, woody, rock/bare ground, or herbaceous in two 2 × 2 m plots randomly placed on the transect along each side of the net lane. We measured basal area with a 10-factor prism from the center of the net lane.

Data Analyses.—We standardized captures for each species per 100 mist-net hrs, where 1 mist-net hr = 1 net open for 1 hr. Bird species that did not breed locally were excluded from analyses, and only first captures of individuals were used. We assigned species to two breeding habitat guilds: early-successional or mature forest based on Ehrlich et al. (1988) and observations from earlier studies in West Virginia (e.g., Duguay et al. 2000). Species were placed into foraging guilds (insectivorous or seasonally frugivorous) based on available life history data (e.g., Birds of North America species accounts) and a cursory examination of fecal samples from captured birds. We performed separate analyses for hatch year (HY = born that spring) and adult (AHY ≥1 year of age) birds; juveniles are usually more susceptible to capture and may use habitats differently than adults. We occasionally caught family groups, but it was a small percent of overall captures (~5%; similar to Marshall et al. 2003), and these age groups were treated independently.

We selected explanatory variables to model bird responses to resource availability that represented the vegetative cover and food resources near nets, the main hypotheses for habitat use. We tested for pairwise correlation among all variables using Pearson's product-moment correlation (Proc CORR; SAS Institute 2003). Percentage variables were arcsine transformed to approximate normality. We reduced the number of explanatory variables within a category (fruit, arthropod, and vegetative cover) by dropping strongly correlated variables ($P \geq 0.7$) to avoid multicollinearity. We selected the one that was less correlated with other model variables or most biologically meaningful when choosing between two correlated variables. Nine variables were retained for modeling (Table 1).

We developed sets of *a priori* candidate models from these nine variables to explain avian capture rates and other metrics of interest based on a review of recent literature on post-breeding bird ecology. The 8–13 models developed for each species or group are described in McDermott (2007). Arthropod biomass was analysis-specific; prey size categories were chosen based on what is known of prey items consumed by each bird species. Total arthropod biomass included all prey sizes when multiple bird species were combined for a particular analysis.

Response variables included capture rates of all adult and HY birds for species captured at >30% of nets or the top four species captured in each habitat guild, and capture rates of each age group classified by diet and breeding habitat (all

TABLE 1. Net-level vegetative and food resource variables used to model bird use of early-successional habitats during the post-breeding period in northcentral West Virginia, 2006. Resources were sampled concurrently with mist-netting from late-June through mid-August.

Variable	Code	Value range	$\bar{x} \pm$ SE
Vegetative cover			
Understory stem density[a]	DENSE	34–282	121.42 ± 3.74
Residual basal area, m^2/ha	BA	0–11.48	3.02 ± 0.24
Vertical complexity index[b]	VCI	42–117	74.92 ± 0.98
Fruit resources[c]			
Fruit abundance	FRUIT	95–4,408	802.07 ± 41.57
Total ripe fruit	RIPE	0–846	18.65 ± 5.29
Arthropod resources[d]			
Arthropod richness, number of Orders	RICH	5–12	8.33 ± 0.11
Total arthropod biomass, mg	ARTH	15.3–407.9	100.04 ± 5.46
Lepidopteran larval biomass, mg	LEP	0–373.3	16.19 ± 2.25
Seed resources			
Herbaceous ground cover, %	SEED	3–100	47.6 ± 1.97

[a] Number of stems <7.6 cm dbh at two 2 × 2 m plots on either side of each mist-net lane.
[b] Vertical complexity index calculated as a sum of all canopy cover class percentages divided by 100 and multiplied by 20.
[c] Fruit was measured along two 12 × 1 m transects on either side of each mist-net lane.
[d] Arthropods were sampled with a beating technique at 4 shrubs/net.

seasonal frugivores and insectivores by habitat guild). We only analyzed age classes with ≥20 captures. A small percentage of adults met strict criteria for post-breeding (only one-third were not in full breeding condition and were actively molting); we included all adults captured during this period including late-breeders (30%) for both breeding habitat guilds. We analyzed molt score index and body condition in addition to the individual species and groups.

Adult molt score (0–250; Cherry and Cannell 1984) was reclassified to values of 0–6. We did not analyze molt score as continuous because birds with a score of 0 or 250 are not molting flight feathers; these scores were reclassified as 0 because these birds would be similarly capable of flight. Adults in the heaviest stage of molt (score = 100–140) are most likely to have compromised flight and higher energetic demands (Jenni and Winkler 1994); they received the highest reclassified value (6). Each HY individual was given a molt score of 0–3 depending on the number of feather tracts in pin.

Body condition was calculated by dividing mass (g) by wing length (mm) to account for body size (Winker 1995). Mass was regressed against wing length for each species, and the residuals were used as the condition index. These values were reclassified to a score of 0–4.

We used Poisson regression (Proc NLMIXED; SAS Institute 2003) to model each response variable except body condition, which had a normal distribution and was analyzed with linear regression. This procedure allows for a hierarchical (i.e., nested) approach to account for within-stand variability, and both Poisson and linear distributions can be modeled. Analyses were conducted at the net scale because of variability in food and vegetative resources within stands and to examine microhabitat use patterns.

We used an information-theoretic approach to select the best approximating models from each set of candidate models. The global model for each response variable was constructed using all variables (range = 7 to 9) relevant to each species or group. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) regardless of the sample size:parameter ratio, because second-order AIC_c converges to AIC as n becomes large (Burnham and Anderson 2002). We did not use QAIC to re-rank models, instead including a random effect in the regression models to account for any dispersion problems in the data (SAS Institute 2003). We rescaled the resulting information criteria for each candidate model to obtain Δ_i AIC_c (differences between the top model and every other model) and calculated Akaike weights (w_i) to better interpret the relative

TABLE 2. Number of individuals captured for individual species or groups of species analyzed (in bold) in regression models. Birds were captured by mist nets in northcentral West Virginia, June-August 2006.

Species	Foraging guild[a]	Total captures	Captures[b]	
			AHY	HY
Early-successional species				
Chestnut-sided Warbler	I	309	**123**	**186**
Common Yellowthroat	I	42	**26**	16
Gray Catbird	F	75	**39**	**36**
Indigo Bunting	I	63	**41**	**22**
Early-successional insectivores	I	520	**245**	**275**
Mature-forest species				
American Redstart	I	58	**26**	**32**
Canada Warbler	I	41	18	**23**
Hooded Warbler	I	49	**34**	15
Red-eyed Vireo	I	59	**51**	8
Veery	F	68	**39**	**29**
Mature-forest insectivores	I	440	**227**	**213**
Frugivores	F	225	**136**	**89**

[a] Foraging guilds analyzed were: I = primarily insectivores post-breeding and F = seasonal frugivores.
[b] HY = hatch year (juveniles), AHY = after hatching year (adults).

likelihood of a model. Models with a Δ_i AIC < 2 were given equal consideration as competing models.

RESULTS

We captured 1,189 individuals: 579 HYs and 610 adults of 15 early-successional and 38 mature forest species. Insectivores predominated; seasonal frugivores comprised 20% of species and individuals captured. Total captures per species (by age) or group of species analyzed ranged from 22 to 275 (Table 2).

Early-Successional Bird Habitat Use.—The same cover and food variables were important for both age groups of early-successional insectivores (Table 3). Capture rates were negatively related to vertical complexity (Fig. 1), understory stem density, and basal area. Age groups had opposite relationships to food variables. Adults were positively related to arthropod biomass (Fig. 2) and negatively to Lepidopteran larval biomass, the opposite of HYs.

We analyzed four early-successional bird species including three insectivores (Table 2). Chestnut-sided Warbler (*Dendroica pensylvanica*) captures were poorly predicted by all variables (Table 3). Five models with different variables had a similar likelihood of being selected for adults, while HY capture rates were best explained by the global model. Associations were the same as for all early-successional HY captures pooled because this species comprised 67% of these captures. A negative association with residual basal area best explained Common Yellowthroat adult (*Geothlypis trichas*) captures (Table 3, Fig. 3). Captures of adult Indigo Buntings (*Passerina cyanea*) were best explained by increases in vertical complexity. Several models competed to explain captures of HY Indigo Buntings. Of these, models with vertical complexity and basal area (negative relationships) had the highest collective weights.

Models containing food variables were important for some species (Table 3). Adult Indigo Bunting captures were positively associated with herbaceous ground cover, which may represent availability of seeds. Lepidopteran larval biomass and total arthropod biomass were positive predictors of Chestnut-sided Warbler HY and adult captures, respectively. HY Indigo Bunting captures were positively associated with Lepidopteran larval biomass.

We analyzed one seasonal frugivore in the early-successional habitat guild: Gray Catbird (*Dumetella carolinensis*). Ripe fruit was negatively related to Gray Catbird capture rates (Table 3), and basal area and stem density were positively related to adult captures. The global model best explained HY catbird captures; vertical complexity and basal area were positively related to captures whereas nearly all food variables were negatively related.

TABLE 3. Regression analysis of bird capture rates by species, guild, and age group in northcentral West Virginia, 2006. Relationships with explanatory variables in competing models are presented.

Response variable	Explanatory variables
Early-successional species	
Chestnut-sided Warbler, adults	LEP (−), ARTH (+), BA (+), DENSE (+), VCI (−)
Chestnut-sided Warbler, HY	GLOBAL[a]
Common Yellowthroat, adults	BA (−)
Gray Catbird, adults	BA (+), VCI (+), RIPE (−), DENSE (+)
Gray Catbird, HY	GLOBAL
Indigo Bunting adults	VCI (+), SEED (+), RICH (+), ARTH (+)
Indigo Bunting HY	BA (−), VCI (−), DENSE (−), RICH (−), LEP (+), SEED (−), ARTH (−)
Early-successional insectivores	
Adults	ARTH (+), LEP (−), VCI (−), BA (−), DENSE (−)
HY	GLOBAL
Mature forest species	
American Redstart, adults	DENSE (−), ARTH (+), VCI (+)
American Redstart, HY	VCI (+), ARTH (−), DENSE (+), LEP (+), BA (+)
Canada Warbler, HY	BA (−), ARTH (−), DENSE (−), VCI (−)
Hooded Warbler, adults	ARTH (+), DENSE (+), LEP (+)
Red-eyed Vireo, adults	BA (−), RICH (+), DENSE (−), VCI (+)
Veery, adults	ARTH (+), FRUIT (+)
Veery, HY	VCI (−), RIPE (+)
Mature forest insectivores	
Adults	ARTH (+), DENSE (−), VCI (+), LEP (+), BA (−)
HY	GLOBAL
All frugivores	
Adults	BA (+), RIPE (−), DENSE (−) FRUIT (+), VCI (−)
HY	RIPE (+), BA (+), DENSE (−), VCI (+), FRUIT (+)
Molt index	
Adults	RIPE (+), ARTH (−), VCI (+), BA (+), FRUIT (+), LEP (+), DENSE (+)
HY	FRUIT (+), ARTH (+)
Body condition index	DENSE (−), LEP (−), VCI (+), FRUIT (−)

[a] The global model, in which all variables were used, was the only competing model.

Mature Forest Bird Habitat Use.—Adult insectivore capture rates were best explained by both cover and food variables (Table 3). Capture rates increased with increasing vertical complexity (Fig. 1), total arthropod biomass (Fig. 2), and Lepidopteran larval biomass, and decreased with increasing basal area (Fig. 3) and stem density. The global model best predicted capture rates of HYs. Cover variables had the same relationships as with adults, but arthropod biomass was inversely related to captures of HYs.

Four of five species we analyzed were primary insectivores (Table 2). Cover variables dominated the top models for these species. Vertical complexity was one of the top explanatory variables for both HY and adult American Redstart (*Setophaga ruticilla*) captures; (positive relationship). Red-eyed Vireo (*Vireo olivaceus*) adults were also positively associated with vertical complexity. The basal area model received the most support for captures of HY Canada Warblers (*Wilsonia canadensis*) and adult Red-eyed Vireos (Table 3) showing a negative relationship for these species (Fig. 3). The stem density model received a weight of 13% for Red-eyed Vireo adult captures and 20% for Hooded Warbler (*Wilsonia citrina*) adult captures, but showed opposite patterns: Red-eyed Vireo capture rates declined while Hooded Warbler rates increased with increasing understory stem density.

Food variables were positively associated with captures of several species (Table 3): Lepidopter-

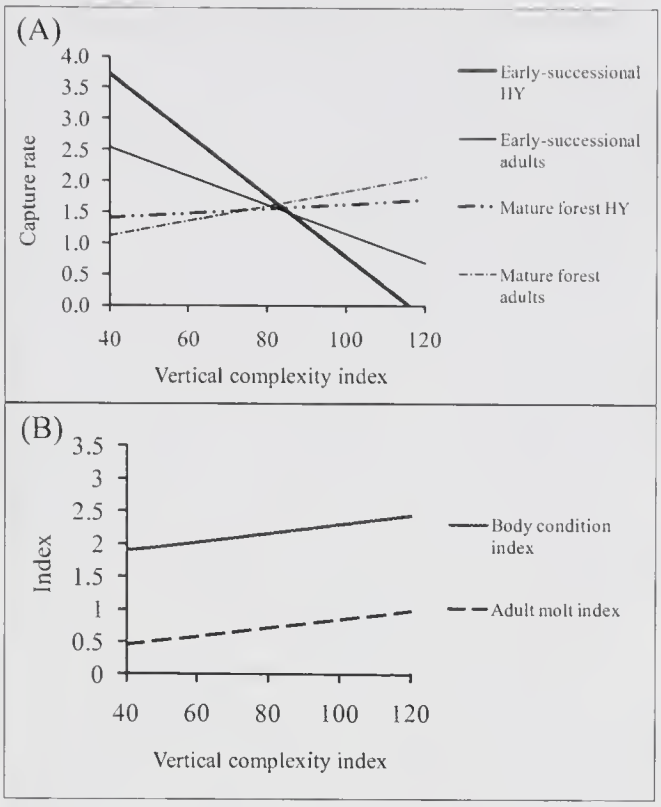

FIG. 1. Relationship of vertical complexity of the vegetation in early-successional habitats of northcentral West Virginia in 2006 with (A) capture rate (captures/100 net hrs) of adult and hatch year (HY) birds of mature-forest and early-successional insectivorous species, and (B) body condition and molt index of captured adults.

an larvae with adult Hooded Warbler and HY American Redstart captures; arthropod richness with Red-eyed Vireo adult captures; and arthropod biomass with American Redstart and Hooded Warbler adults.

The Veery (*Catharus fuscescens*) was the only seasonal frugivore analyzed in the mature forest habitat guild. Adult Veery capture rate was

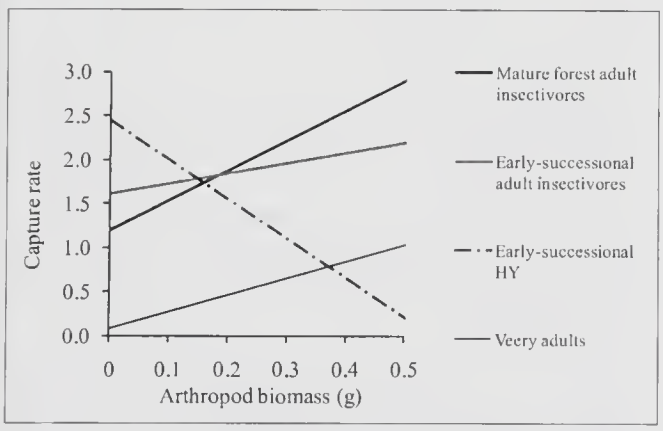

FIG. 2. Captures/100 net hrs as a function of arthropod biomass for all mature-forest and early-successional adult insectivores, adult Veeries (seasonal frugivores), and early-successional hatch year (HY) birds in early-successional habitats of northcentral West Virginia in 2006.

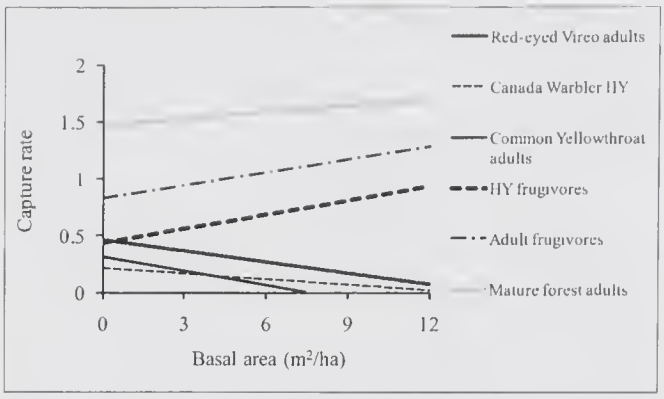

FIG. 3. Relationship between capture rate (captures/100 net hrs) and basal area for HY and adult frugivores, mature forest adults, Red-eyed Vireo adults, Canada Warbler hatch year (HY) birds, and Common Yellowthroats in early-successional habitats of northcentral West Virginia in 2006.

positively associated with arthropod biomass (Fig. 2) and total fruit (Table 3). The model with vertical complexity (negative association) was ranked only 1.5 times better than that with ripe fruit (positive association) for HYs. However, these relationships were weak suggesting inadequate model structure.

Frugivore Habitat Use.—Nine species from different breeding habitat associations represented the seasonal frugivores. Total fruit abundance was positively associated with both age groups but was not a strong predictor in top models (Table 3). Age groups showed opposite relationships with ripe fruit: negative for adults and positive for HYs. The model with basal area (positive association) received 33% of the weight for adults, and basal area was the highest ranked cover parameter when considering all HY bird models (Fig. 3).

Molt Score.—Molting HYs were positively associated with total fruit abundance (Table 3). This model was ~2.5 times as likely to be selected as the model with arthropod biomass (w = 0.11). Abundance of ripe fruit best explained molt score of adults (w = 0.69), but the global model also received support. All cover variables in the global model were positively related to adult molt, and vertical complexity was the highest ranked cover variable when considering all models. Complex vertical structure (a high index value) was associated with individuals in the most compromising stage of molt (Fig. 1).

Body Condition Index.—Cover variables best explained variation in body condition index (Table 3). Low stem density (w = 0.15) and high

vertical complexity (w = 0.15; Fig. 1) best predicted high body condition index values. Arthropod and fruit variables were negatively related to body condition.

DISCUSSION

Predator-Avoidance Hypothesis.—Cover variables were important for post-fledging juveniles and adults using timber harvests. Birds may be selecting habitats with increased vegetative complexity that offers protection from predators. King et al. (2006) found that fledgling Ovenbirds had higher survival rates where understory vegetative structure was greatest. Thus, vertical complexity may be a good representation of protective cover.

Thicker cover as measured by understory stem density had a negative influence on bird captures. Similarly, Vitz and Rodewald (2007) found a negative relationship between mature forest bird capture rates and density of shrub vegetation. Birds in our study were often traveling in foraging flocks that contained several species, and an open understory would facilitate movement of individuals.

Adult Chestnut-sided Warblers, Gray Catbirds, and Hooded Warblers, species that nest in the harvested areas (McDermott 2007), had higher capture rates at nets with more understory stems. Thus, a higher understory stem density could serve as protective cover during nesting and post-breeding for these species. Early-successional bird habitat use outside of breeding tends to be less flexible than for those species nesting in mature forest (Rodewald and Brittingham 2004). Stand-level variables such as area and amount of edge (McDermott 2007, Schlossberg and King 2008) may explain more variation in habitat use by those species nesting in shrub-scrub.

Residual trees in two-aged stands inhibit understory growth and limit stem density (Miller et al. 2006), but leave-trees provide raptor perches and residual trees may not offer predator protection. This suggestion is supported by our data as captures were negatively associated with basal area; within stands, captures were greater at nets with fewer nearby trees.

Resource-Selection Hypothesis.—This study provides evidence that post-breeding habitat use is influenced by food resource availability. For example, arthropod biomass positively predicted captures of adult insectivores and Veeries, which, like other seasonal frugivores, also consume arthropods. Lepidopteran larval biomass was a positive predictor of mature forest (e.g., Canada and Hooded warblers) and early-successional HY captures. Lepidopteran larvae are an important food source for nestling and adult songbirds (Van Horne and Bader 1990, Jones et al. 2003). Shrub-dwelling Lepidopteran larvae may have higher biomass in clearcuts than in mature forest because deciduous shrubs have high amounts of foliage (Van Horne and Bader 1990, Keller et al. 2003). Thus, some birds, especially mature forest individuals, may be keying on this rich energetic source within early-successional habitats. Arthropods may be a fleeting resource because biomass is significantly higher in young clearcuts when they become fully stocked (by year 6 or 7) versus later seral stages (Keller et al. 2003).

We found few strong relationships with total fruit abundance. Similarly, Vitz (2008) did not find evidence that mature forest birds use clearcuts for fruit resources. White et al. (2005) found a positive relationship between thrush habitat use and fruit abundance, but we found only a weak positive relation for the Veery, the only thrush species analyzed individually in our study.

We included herbaceous cover as a crude index of seed availability for seed-eating birds in the models. Indigo Bunting captures, particularly adults, were explained best by herbaceous cover. Thus, herbaceous plants may serve as a cue for seed availability for granivores.

We found limited evidence for the resource selection hypothesis. We do not know accurately what constitutes available food for a bird without behavioral observations to quantify food resource selection (Hutto 1990). Foliage-associated arthropod biomass may have misrepresented available food, despite adjusting for potential prey size differences. Birds may not be able to key in on food resources at the net scale because of high within-stand variability in arthropod communities. We do not know how or if food is limiting during the post-breeding period. Food limitation likely varies from year to year and is more likely to occur during breeding because of food requirements of rapidly growing nestlings (Nagy and Holmes 2005).

Food and Cover Related to Condition, Molt, and Age.—The physical condition of a bird in theory is positively related to food resources and deposited body fat. However, food resource availability in our study was negatively associated with body condition of captured birds. Instead, a high index value was associated with high vertical

complexity. One explanation is that birds with a higher body condition index may use the most structurally complex habitat, which we infer offers the best protection and increases likelihood of survival. Birds in poor condition may select habitat with rich food resources to replenish fat reserves, while birds in better condition select microhabitat that provides protection from predators (Moore and Aborn 2000). Habitat use may depend on physical condition, and both cover and food resources are important for post-breeding survival, which is influenced by body condition of fledglings in some species (Krementz et al. 1989, Naef-Daenzer et al. 2001). There was no evidence that body condition increased over the season; we sampled prior to pre-migratory fattening, and the mean condition index decreased over time due to a concomitant increase in HY captures.

Age-specific differences were evident for most of the groups analyzed, particularly with food variables. Adults had a higher body condition index than juveniles for most species analyzed (MEM, unpubl. data), which may have contributed to these differences. HY capture rates were negatively associated with arthropod biomass, while adult capture rates had a positive relationship. HYs are likely inexperienced in recognizing arthropod availability cues and may have a lower foraging efficiency than adults (Stevens 1985, Weathers and Sullivan 1989, Vanderhoff and Eason 2008) and thus, lower survival. These data bolster the argument that adults and HYs may be keying on different features within a stand, which may account for age-specific survival rates during the post-breeding period.

Molting birds likely take advantage of both food and cover. Adults in heavy molt with diminished flight capabilities were associated with high vertical complexity, which likely provides protection from predators. Molting birds were positively associated with fruit variables. Changes in food choice have been observed in the field for molting passerines, and food availability may influence the timing and place of molt (Jenni and Winkler 1994). Increased energy requirements during molt could be fulfilled by an abundance of fruits for the 13% of molting adults and 15% of molting juveniles that were frugivorous or, for insectivores, an abundance of arthropods that are attracted to fruits (Sallabanks and Courtney 1992).

Early-successional habitats, including those retaining canopy trees such as the two-age harvests we sampled, should be recognized for their conservation value. Avian survival may be compromised by ignoring bird habitat requirements outside of breeding (King et al. 2006). Habitat use does not imply habitat quality; a variety of parameters (relative abundance, survival, body condition) should be measured to evaluate post-breeding habitat quality for birds.

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DISTRIBUTION, ABUNDANCE, AND STATUS OF CUBAN SANDHILL CRANES (*GRUS CANADENSIS NESIOTES*)

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ABSTRACT.—We conducted the first country-wide survey between 1994 and 2002 to examine the distribution, abundance, and conservation status of Sandhill Crane (*Grus canadensis nesiotes*) populations throughout Cuba. Ground or air surveys or both were conducted at all identified potential areas and locations previously reported in the literature. We define the current distribution as 10 separate localities in six provinces and the estimated total number of cranes at 526 individuals for the country. Two populations reported in the literature were no longer present and two localities not previously reported were discovered. The actual number of cranes at two localities was not possible to evaluate due to their rarity. Only four areas (Isle of Youth, Matanzas, Ciego de Avila, and Sancti Spiritus) each support more than 70 cranes. The remaining locations each have less than 25 individuals. Sandhill Cranes appear to be declining and have almost disappeared in Pinar del Rio and Granma provinces, and in northern Matanzas Province. Identified threats to the remaining populations include habitat modification (woody plant encroachment, agricultural expansion, and fire suppression), predation due to wild hogs (*Sus scrofa*), dogs (*Canis lupus familiaris*), mongoose (*Crossarchus* spp.), and poaching. *Received 3 November 2009. Accepted 11 February 2010.*

The Cuban subspecies of Sandhill Crane (*Grus canadensis nesiotes*) is one of many endemic bird subspecies and species present in Cuba. Little information regarding distribution or overall ecology (Meine and Archibald 1996) has been published recently or historically on this rare crane despite being one of the largest birds in the country, and the Caribbean. The Cuban Sandhill Crane has unique characteristics relative to the other subspecies. For example, most nests are constructed on dry land (Walkinshaw 1953, Galvez Aguilera et al. 2005), which differs from all other subspecies which nest primarily in association with wetlands (Tacha et al. 1992). The Cuban subspecies of Sandhill Crane is listed as critically endangered (IUCN 1994). Only four populations were known in the early 1990s and the population for Cuba was estimated at between 100 and 200 individuals by different authors.

The first records of Sandhill Cranes in Cuba are from Poey (1851–1855) and Gundlach (1875, 1876) who described the distribution of this species in large savannahs in Cienega de Zapata and pine (*Pinus* spp.) -dominated savannahs east of Guamutas and on the Isle of Pines (currently named Isle of Youth). Barbour (1943) reported cranes from south of Matanzas Province near Alacranes and Union de Reyes. Bangs and Zappey (1905), Read (1913), Walkinshaw and Baker (1946), and Garrido (1985) described the distribution on the Isle of Youth (Pines) as limited to open plains north of Cienega de Lanier. Walkinshaw (1953) defined the distribution on the Isle of Youth as encompassing the region north of Cienega de Lanier from Siguanea westward to West Port and eastward to Pasadita. They are reported to extend to Sabana Grande on the Isle of Youth during winter. Garcia (1987) summarized the status of endemic subspecies in Cuba and considered cranes rare in all regions where they were previously considered abundant, such as in Guane, Mendoza, and Vinales. Garcia (1987) emphasized the need to protect cranes where they were still present at that time, including Pinar del Rio, Ciego de Avila, Camaguey, Cienega de Zapata, and the Isle of Youth.

The presence of Sandhill Cranes has been documented over time in different regions of Cuba; however, few authors have made quantitative estimates of their abundance. The most documented population is that on the Isle of Youth. The status of Cuban Sandhill Cranes in Cuba at the beginning of our field work was not well known and many different estimates of crane numbers had been put forward from a low of 100 to a high of "about" 300 individuals (Meine and Archibald 1996). There have been reports over the past several years on the population size of cranes by different authors, although they are not in agreement. Cuban Sandhill Cranes, from the time

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Gundlach (1875) made his observations when cranes were believed to have been "plentiful", are considered to have decreased (Walkinshaw 1953). Cranes were considered to be more common during the mid 1980s than formerly (Garrido 1985), suggesting that numbers had increased between the 1950s and 1980s. Walkinshaw (1953) suggested that during the early 1950s, Sandhill Cranes had almost disappeared from mainland Cuba. Numbers reported for Cuban Sandhill Cranes have fluctuated from 200 in 1953 (Walkinshaw 1953) to 120 in 1975 (Garrido and Garcia 1975) to more than 200 individuals in the early 1990s (XGA, pers obs.). Most reports citing numbers of cranes in Cuba are estimates based on only limited field research or field surveys, which we believe underestimated actual crane numbers.

Many of the 15 crane species, and several subspecies of more common cranes, are considered to be threatened or endangered (Meine and Archibald 1996). The Cuban Sandhill Crane at the beginning of our work was considered to be critically endangered per the IUCN Red List (IUCN 1994), likely because no reliable information on numbers and distribution was available. The critically endangered designation was based on the belief the populations present were highly fragmented and each numbered less than 50 individuals. We undertook a study to evaluate the current status of the Cuban subspecies of Sandhill Crane in 1995 due to lack of reliable recent information and disagreement among different literature sources on distribution and abundance. Our overall objective was to define the distribution and estimate abundance of the Cuban Sandhill Crane throughout the country. Our specific objectives were to: (1) identify the presence and distribution of different population(s) or subpopulations of this subspecies in Cuba, (2) estimate the number of individuals present at each separate location or population, and (3) evaluate the status and potential conservation problems for each of the distinct populations.

METHODS

Country-wide Surveys.—We initially planned a nation-wide search; however, the entire country is not suitable for cranes and we limited our field surveys to areas deemed appropriate based on vegetation characteristics, topography, and personal knowledge of different areas. A preliminary evaluation of Sandhill Crane distribution was defined by contacting field personnel of the Empresa Nacional para la Proteccion de Flora y Fauna (National Agency for the Protection of Flora and Fauna, hereafter Flora and Fauna) to identify areas where cranes had been observed in the previous 5 years. Areas reported in the literature as having cranes were included for preliminary evaluation, regardless of whether new or recent observations had been reported. Each site believed to have potential for cranes was visited and presence was confirmed through actual sighting of cranes from air or ground surveys. The number of cranes present at selected sites in each area was estimated from intensive and extensive ground counts.

Aerial surveys were conducted throughout a large portion of the country in areas described on vegetation maps as having characteristics of potentially suitable habitat for Sandhill Cranes (open areas, savannahs, and sparsely forested areas). Open habitat types in Cienega de Zapata, and the provinces of Isle of Youth, Sancti Spiritus, and Camaguey were surveyed at low altitudes (40–60 m) during October 1995 using a fixed-wing airplane. Areas in the provinces of Pinar del Rio, Cienega de Birama, and the northern regions of Matanzas were surveyed from the air in January 1996.

Areas in each province with appropriate vegetation characteristics, or actual sightings following the aerial surveys, were visited to conduct personal interviews with local inhabitants. Three hundred and forty interviews were conducted of between 10 and 20 individuals in each potential region who had lived in the area at least 20 years. Those interviewed included employees of Flora and Fauna, forest rangers, fishermen, farmers, cattle producers, and others who spent much of their time outdoors in areas likely to be used by cranes. Areas where interviews indicated cranes were likely to be present were surveyed extensively by driving and walking routes to estimate the number of cranes present. More intensive and standardized counts were conducted in areas where cranes appeared to be abundant, or widespread.

Population Estimates.—Coordinated point counts were conducted in four areas that appeared to support the largest numbers of cranes to define their distribution and estimate population size. All counts were conducted during February between 1995 and 2002 with a different area sampled each

TABLE 1. Cuban Sandhill Crane populations by location and province.

Province	Location	Population[a]	Estimated number	Status	Protected by[b]
Pinar del Rio	Guane	1	<10	Stable	ENPFF/CGB
	Consolacion Sur	2†	0	Extirpated	NA
Matanzas	Cienega de Majaguillar	3	<12	Unknown	ENPFF
	Cienega de Zapata	4	120	Increasing	EFI/(AP)
Sancti Spiritus	Cienega de las Guayaberas	5	71	Stable	ENPFF (AP)
Ciego de Avila	Moron Norte	6	102	Stable	ENPFF (AP)
	Jucaro	7	Present	Stable?	ENPFF
Camaguey	Sabana de Lesca	8	24	Stable	CGB
	Cayo Romano	9	16	Unknown	ENPFF (AP)
Granma	Cienega Birama	10†	?	Not confirmed	ENPFF (AP)
Isle of Youth	Los Indios (11) and Sabana Grande (12)	11, 12	171	Increasing	ENPFF (AP)

[a] Figure 1.
[b] ENPFF = Empresa Nacional para la Proteccion de Flora y Fauna (National Agency for the Protection of Flora and Fauna), EFI = Empresa Forestal Integral (Integrated Forestry Agency), CGB = Cuerpo de Guardabosques (Forest Ranger Corps), AP = Protected Area.
† = not confirmed.

year. Methods used for counts were those developed by the International Crane Foundation and used in Wisconsin (Meine and Archibald 1996) and Mississippi (Hereford et al. 2001) for other subspecies of Sandhill Cranes. Counts were conducted by systematically establishing observation points 1.5–2 km apart throughout the entire area to be sampled. Ground counts conducted in the four areas with the largest numbers of cranes consisted of between 16 and 40 points. Two to four observers at each point recorded the number of cranes observed, time of observation, direction from observation point, and direction of flight. Between 300 and 500 persons participated in the counts at each location surveyed. Two hours of observation were conducted before sunset during an evening followed by 2 hrs of observation the next morning beginning at sunrise.

We recorded number of birds seen, time of observation, and direction of flight at each sample location to eliminate duplicate observations. The maximum number of birds, after eliminating duplicate counts, was considered the total for that area.

RESULTS

Distribution and Abundance.—We defined the distribution of Cuban Sandhill Cranes as consisting of 10 separate localities and presumed to consist of nine separate populations in six provinces (Table 1, Fig. 1). We estimated 526 cranes for the entire country. The total cranes counted in each of the areas with largest numbers of cranes varied from 71 in Guayaberas to 171 on the Isle of Youth (Table 2) for a total of 464 cranes in the four areas with the largest populations. We estimated all other sites combined to have 62 cranes (Table 1) based on site visits,

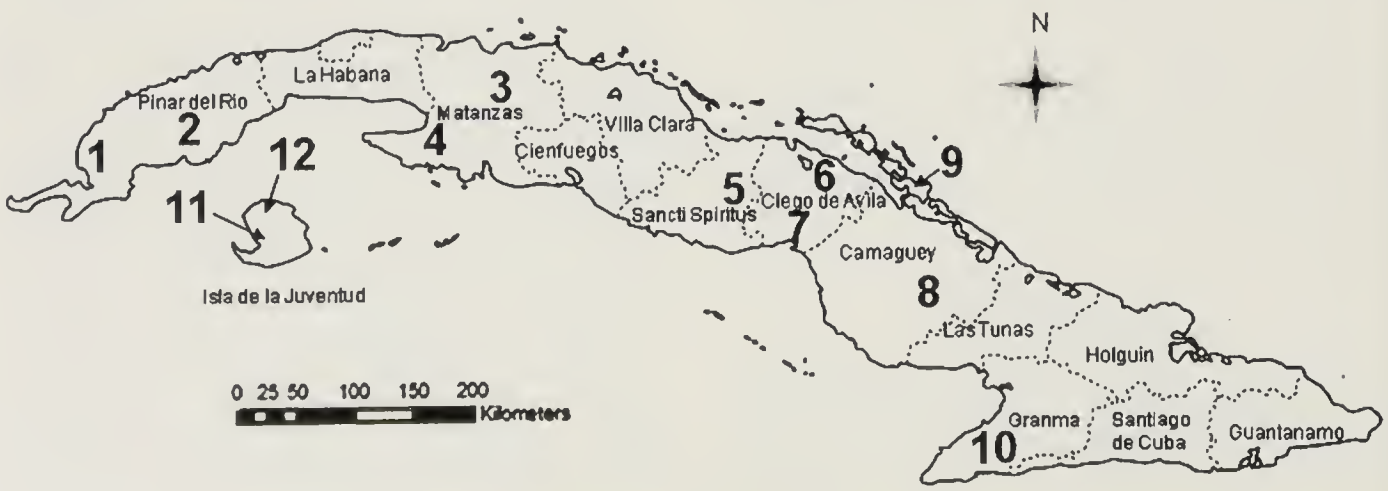

FIG. 1. Distribution of Sandhill Crane populations in Cuba. Numbers represent the location of populations corresponding with data in Table 1.

TABLE 2. Estimates of Sandhill Crane abundance in the four largest populations in Cuba.

Category	Isle of Youth	Cienega de Zapata	Guayaberas	Moron Norte
Survey period	February 1998	February 1999	February 1998	February 2002
# Count stations	52	26	16	32
Cranes obs./point	5.3	6.3	9.1	6.5
Range	1–22	1–21	4–16	2–18
Estimated total cranes	171	120	71	102

ground-based surveys, direct observations, and knowledge of local people. We confirmed crane presence for Jucaro (#7, Fig. 1) but have no estimate of abundance.

We could not confirm presence of cranes during our study or based on local people's knowledge, for two locations previously reported (Walkinshaw 1949). These included the region of Consolacion del sur in Pinar del Rio Province and Cienega de Birama in Granma Province (#'s 2 and 10, respectively; Fig. 1). Only a rough estimate of numbers is available for two other localities due to the rarity of crane observations in those areas. These localities are Cienega de Majaguillar in northern Matanzas Province and Cayo Romano key, off the northern coast of Camaguey Province (#'s 3 and 9, respectively; Fig. 1).

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Pinar Del Rio Province.—Interviews with 30 local residents suggested crane presence in a small area over the entire time period they could remember. We confirmed crane presence in 1996 in the area of Guane (#1, Fig. 1) with no more than 10 individuals likely remaining. Locals suggested cranes were more common through the 1990s but had decreased significantly in recent years. Large areas were planted with Carribean pine (*Pinus caribaea*) in the 1970s, which apparently caused many areas to become wooded and less suitable for cranes. Our last visit to the area in 2002 confirmed the presence of one chick; however, even fewer cranes were apparent than in 1996.

Threats to cranes in this province include habitat modification, presence of large agricultural operations including hog (*Sus scrofa*) farming, and extensive hunting activities, some of which are reported to be illegal. The area where cranes are present is under management and protection by Forestry Agency authorities, and hunting has been limited due to concerns expressed to authorities regarding the critical situation for cranes in the area. However, the low number of cranes present and the small area of habitat available will make it difficult for cranes to increase in this locality in the future.

Matanzas Province.—Cienega de Zapata (#4, Fig. 1) in the southern portion of the province has long been known to support cranes. Crane presence was confirmed from aerial surveys in 1995 and, in 1996, five nests were found in different sections of the wetlands. We estimated 120 cranes during the ground point counts conducted in Cienega de Zapata in 1998. We recorded a new locality in the northern area of the province not previously reported as supporting cranes called Cienega de Majaguillar (#3, Fig. 1) with an estimate of <12 cranes. The situation of these cranes appears to be similar to that of the precarious population in Pinar del Rio.

There are several threats to cranes in this area. There is loss of open savannah due to increases in woody shrubs and trees such as cayput (*Galaleuca quinquenerva*), believed to be a consequence of decreased use of prescribed fires since the 1970s. Significant populations of wild hogs and dogs (*Canis lupus familiaris*) are present and could threaten Sandhill Cranes.

Sancti Spiritus Province.—Sandhill Cranes are present in the Cienega de Guayaberas and, according to those interviewed, have been present for at least 40 years (#5, Fig. 1). A ground point count conducted in 1998 estimated 71 cranes. The area suitable for cranes is <12 km^2 and is decreasing due to invasion by exotic woody plants such as marabou (*Dichrostachys glomerata*), which eliminates open spaces. Large areas have also been modified for rice cultivation and this practice continues to increase. The presence of water buffalo (*Bubalus bubalis*) has caused overgrazing in some areas further contributing to invasion of exotic woody plants.

Ciego de Avila Province.—Sandhill Cranes have been reported in this province since the beginning of the 20th century. Crane presence was

confirmed via aerial and ground surveys in 1995 and 1996 in the northern portion of the province (#6, Fig. 1), but not in the south (#7, Fig. 1). We did not obtain a count of cranes in the south but did confirm their presence. We estimated 102 and 101 cranes were present in the northern area of the province based on point counts conducted in 1997 and 2002, respectively. Chicks were observed in this area in 1995 and 1996. Northern Ciego de Avila supports one of the largest populations of cranes in Cuba and is a priority area for protection. The case for protection was made to government authorities. A 250,000-ha protected area was established in summer 2004 that will limit and control expansion of habitat alterations in the entire region. However, agriculture, cattle grazing, and tree plantations continue and could affect crane habitat in the future.

Potential threats in this area include extensive livestock grazing, exotic plants and animals, and habitat fragmentation due to agriculture and tree plantations. Cattle grazing is expanding and there is an effort to establish non-native grasses for livestock forage. Feral water buffalo are present, which has led to overgrazing and erosion in some areas. Invasive plants include casuarina (*Casuarina equisetifolia*) and marabou, which are rapidly increasing and causing reduction of open savannahs. The hydrological regime of this area has been affected by deforestation of native plants, road construction, and sugar cane fields, which could flood crane nests and drown chicks. The presence of sugar cane fields provides cover for mongoose (*Crossarchus* spp.) and black rats (*Rattus rattus*), which depredate crane eggs.

Camaguey Province.—Historical Sandhill Crane localities (#8, Fig. 1) in this province included Sabanas de Lesca and Meseta de San Felipe. Surveys of local people suggested cranes were no longer present but we observed six cranes flying in 1994. At least 12 pairs were observed in a 2001 ground survey in the Meseta de San Felipe. A previously unreported area was key Cayo Romano off the northern coast (#9, Fig. 1), which is believed to have had cranes for at least 30 years. No extensive count was possible during our work in this area but biologists who visited the site estimated that ~16 cranes are present on this key.

Principle threats in this area include possible future mining activities and military exercises (Cayo Romano) that occur in the area occupied by cranes. Wild dogs are known to be present in the area.

Granma Province.—A single recent visual observation was reported in interviews for this province in the region of Birama in the delta of Rio Cauto (#10, Fig. 1). Interviews suggested cranes were common in the 1970s through the mid 1980s, but decreased in number through the early 1990s and are now believed to be completely absent. Our ground searches conducted yearly between 1999 and 2002 could not confirm the presence of cranes in this area. Habitat modifications in areas of previous crane use include development of wetlands for rice production. We believe cranes have been extirpated from this province.

Isle of Youth Province.—Isle of Youth is a well known area for Cuban Sandhill Cranes (#'s 11 and 12, Fig. 1). The type specimen for this subspecies was collected from the Isle of Youth (Bangs and Zappey 1905). Two ground counts were conducted on the Isle of Youth using the same points in 1995 and 1998, yielding estimates of 115 and 171 cranes, respectively. The 1995 value is similar to that reported by Walkinshaw (1953) of 100 cranes for the Isle of Youth. We believe the 1998 count is more accurate as it was conducted over 2 days during one morning and one afternoon, compared to the 1995 count which was conducted only during the morning.

Threats present include cattle grazing activity and herding during the nesting period. Illegal hunting and fishing activities cause disturbance to the cranes in this area.

Conservation Status of Populations

Eight of 10 areas supporting Sandhill Cranes are under some form of protection, either as protected areas or other schemes managed by Flora y Fauna. These include Birama, Cayo Romano, Norte de Moron, Cienega de Guayaberas, Cienega de Zapata, Majaguillar, Jucaro, and Los Indios/Sabana Grande. Two more were under management by the Forestry Agency in Matanzas Province (Empresa Integral Forestal de Cienega de Zapata). Areas where Sandhill Cranes were present in Guane in Pinar del Rio Province and Lesca in Camaguey Province were also managed by the Forestry Agency.

DISCUSSION

We confirmed Cuban Sandhill Cranes to be more widespread than previously reported (Garrido 1985, Garcia 1987, Meine and Archibald 1996). However, presence of cranes in two areas

that previously supported them (Walkinshaw 1949) could not be confirmed. The abundance of cranes estimated during this study for Cuba is higher than all previously reported estimates, leading to reclassifying the Cuban Sandhill Crane from critically endangered in 1994 to vulnerable in 1997. Our estimate of 526 cranes is significantly greater than the estimated 103 individuals of the endangered Mississippi Sandhill Crane (*Grus canadensis pulla*) (Hereford et al. 2001), but lower than the 4,000–6,000 estimated for Florida Sandhill Cranes (*G. c. pratensis*) (Tacha et al. 1994).

The present distribution is broader than expected, but at least two previously documented sites appear to no longer support cranes. We have no explanation for causes of the disappearance of Sandhill Cranes from these areas, except to note significant habitat changes have occurred in those areas. A series of threats was identified for all of the present populations. At least two populations, those in Guane in Pinar del Rio and Birama in Granma, are so low that it is likely they have already disappeared or will do so soon. The estimates are unreliable for other localities and are possibly optimistic, and should be re-evaluated in the field (Cayo Romano and Sabana de Lesca in Camaguey, and Majaguillar in northern Matanzas Province).

We could not identify causes of population disappearance or decreases, but important factors may include population isolation effects and degradation and decreases in available habitat. Decreases in size or fragmentation of habitat could contribute to population declines in some areas as alterations are visible throughout the entire country. The Mississippi Sandhill Crane's low productivity and endangered status is attributed in large part to habitat fragmentation (Valentine 1970; S. G. Hereford, pers. comm.). All existing populations are separated by distances greater than the longest known dispersal movement by non-migratory Sandhill Cranes (up to 48.3 km in Florida; Nesbitt et al. 2002). We have limited data on potential movements and dispersal of Cuban Sandhill Cranes but, of 10 radio-marked birds on the Isle of Youth, a single crane moved >18 km during 1 year (Galvez Aguilera 2002). Even shorter movements (10.5 km by Florida Sandhill Cranes in Georgia; Bennett 1989) are reported for other non-migratory Sandhill Cranes.

Four significant populations appear to be stable and perhaps increasing: (1) Isle of Youth, (2) northern Ciego de Avila, (3) Cienega de Zapata in Matanzas, and (4) Cienega de Guayaberas in Sancti Spiritus. Delineation of a new 250,000-ha protected area in 2004 that encompasses all crane areas in northern Ciego de Avila Province resulted in the four largest populations being at least partially within the boundaries of a protected area. However, that does not guarantee protection as several threats are present regardless of whether they are in or outside a protected area boundary. Woody plant encroachment continues in many areas within Reserves, due to elimination of natural fire regimes, and is a serious problem of concern for several federal agencies (FC-R, pers. obs.). Feral domestic (hogs and dogs) and introduced animals (mongoose) continue to be threats to nesting cranes in all four areas; however, the exact effect of each one of these predators has not been quantified. Predation is a problem that affects other non-migratory populations and is the major cause of mortality for the Mississippi Sandhill Crane (S. G. Hereford, pers. comm.)

We have been working directly in the Isle of Youth over the last few years and recently in Ciego de Avila to better evaluate the specific threats to cranes and develop appropriate or responsive management plans. Some Reserve personnel are trying to implement counts at regular intervals to document population trends. The trend and conservation status of Cuban Sandhill Cranes may not be entirely known until we can ascertain whether numbers are increasing or decreasing over time. Possible direct actions to enhance declining populations could include exchange of individuals from one population to another or from potential captive breeding efforts. Captive breeding programs for cranes do not exist in Cuba, but are present and successful in other countries. Indirect actions to expand or improve nesting habitat could include management activities including instituting prescribed fire programs, and elimination and management of invasive woody plants, as has been done for the Mississippi Sandhill Crane (Valentine and Hereford 1997). Limiting agriculture and forestry plantation expansion in protected areas where cranes are present could also help expand or improve nesting habitats. Control of potential domestic and introduced predators is another action that could be taken in areas where predators are a problem.

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THE FEATHER STRUCTURE OF DIPPERS: WATER REPELLENCY AND RESISTANCE TO WATER PENETRATION

ARIE M. RIJKE[1,2] AND WILLIAM A. JESSER[1]

ABSTRACT.—Dippers (Cinclidae) are the only passerines that find their prey almost exclusively under water. We examined the breast feathers of the five species of dippers for barb diameter and spacing. These results were compared with those measured for other bird families, both aquatic and terrestrial, to detect the presence of any adaptation in the structure of their plumage to their aquatic lifestyle. Barb diameters ($2r$) were about the same for all dipper species at ~25 μm, but spacing ($2d$) varied from ~150 to 215 μm. Dipper feathers exhibited large values for $(r+d)/r$, the structural requirement for excellent water repellency, comparable to that of many other terrestrial birds including starlings (Sturnidae), swifts (Apodidae), and nightjars (Caprimulgidae). A slightly improved resistance to water penetration, indicated by a smaller value for $(r+d)/r$, was observed for White-throated Dipper (*Cinclus cinclus*), whereas increased water repellency was found for both American (*C. mexicanus*) and Brown dippers (*C. pallasii*). Each of these three species is known to dive. No adaptations were observed for White-capped (*C. leucocephalus*) and Rufous-throated (*C. schulzi*) dippers, neither of which dive. The breast feathers of dippers have evolved excellent water repellency, but diving dippers show further adaptations for improved resistance to water penetration and water repellency to allow under-water foraging. *Received 2 November 2009. Accepted 8 March 2010.*

Dippers are the only passerines that find their prey almost exclusively under water. The White-throated Dipper (*Cinclus cinclus*), Brown Dipper (*C. pallassi*), and American Dipper (*C. mexicanus*) habitually plunge into shallow streams and lakes to search for food among rocks, boulders, and vegetation whereas the White-capped Dipper (*C. leucocephalus*) and Rufous-throated Dipper (*C. schulzi*) only dip their heads under water to catch prey detected from their rocky perch. All species, however, are exposed to continuous spray and traverse sheets of falling water with surprising abandon (Ormerod and Tyler 2005).

That feathers of aquatic birds are well adapted to specific foraging habits has been known for some time (Rijke and Burger 1985). For example, the water repellency of feathers, i.e., the ability of water drops to 'pearl' and roll off, is reduced relative to that of terrestrial birds. Further, resistance of feathers to water penetration, i.e., the pressure required to force water between the barbs and barbules, is often increased. The extent of both water repellency and resistance to water penetration can be ascertained by measuring the diameters of the barbs and barbules and their respective separations, which have been quantified for ~150 aquatic and terrestrial species of 45 families (Rijke 1970, Elowson 1984).

Water repellency can be conveniently expressed by the contact angle θ, defined as the angle between the tangent to the curved water surface at the point of contact with the solid surface and the plane of the surface on which the drop is resting, measured through the water (Fig. 1A). If the surface is not smooth, but rough or porous, the drops may entrap air in the hollows and interstices, forming additional air-water interfaces, which will cause considerable increase in the contact angle (Fig. 1B), according to:

$$\cos\theta_a = f_1\cos\theta - f_2 \qquad (1)$$

where f_1 is the area of solid-water interface and f_2 is the area of the water-air interface per unit of apparent surface area. For water drops on barbs, f_1 and f_2 can be expressed (Cassie and Baxter 1944) as:

$$f_1 = (\pi-\theta)r/(r+d) \qquad (2a)$$

and

$$f_2 = 1 - r\sin\theta/(r+d) \qquad (2b)$$

where $2r$ represents the diameter of the barbs measured in the plane of the long axes of the barbs which are separated by distance $2d$ (Moilliet 1963). The increase in apparent contact angle is ascertained only by the parameter $(r+d)/r$ and not by the separate values of r and d. Thus, the apparent contact angle for values of this parameter ranging between 2.4 (penguins, Spheniscidae) and 6.0 (ducks, Anatidae) would vary between ~126° and 146°. These values are significantly higher

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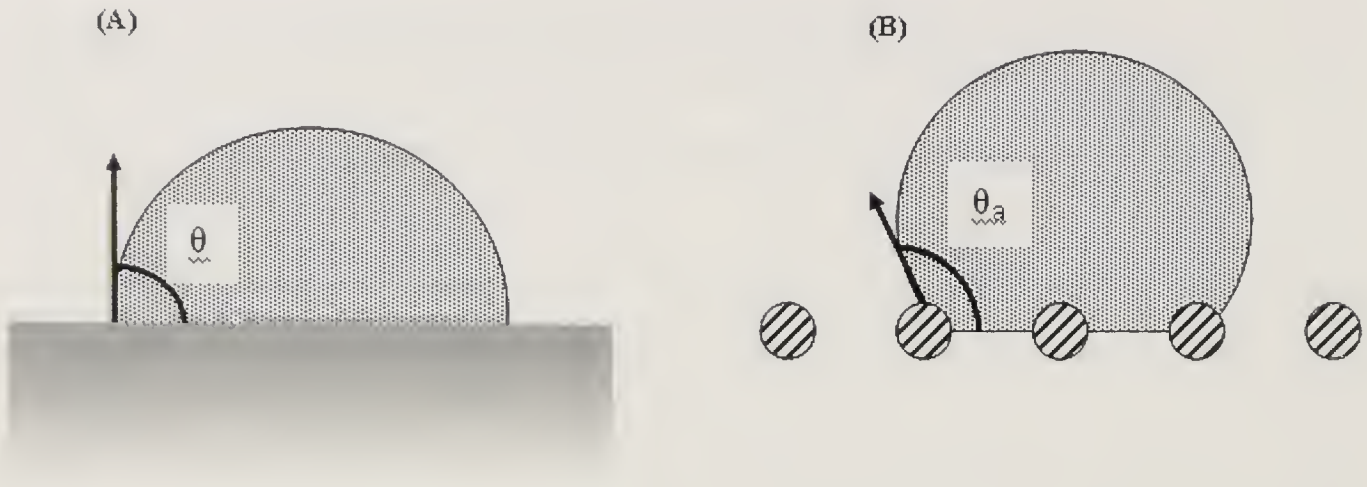

FIG. 1. Schematic of a drop of water, sufficiently small to not be perturbed by gravitational forces, on a smooth surface (A) and a porous surface (B) covered with a repellent waxy film. A contact angle of 90° is measured on the smooth surface covered with preening oil. This angle is increased to ~115° on the porous surface as a direct result of the formed air-water interfaces.

than those attained for the most repellent of smooth surfaces, which equal 114° (Moilliet 1963).

An expression for the pressure (P), required to force water between the barbs and barbules can be derived from premises similar to those above (Moilliet 1963) and is:

$$P = \gamma/r\left\{\cos\theta + \sqrt{[(r+d)/r]^2 - \sin^2\theta}\right\} \quad (3)$$

where γ represents the surface tension of water. Equation 3 shows that P will increase if both r and $(r + d)/r$ are decreased. The requirement of relatively small values for $(r + d)/r$ to provide sufficient resistance to water penetration is opposed by the need for large values for this parameter to attain good water repellency. Thus, the structural characteristics compatible with optimal water repellency are, at least in part, in conflict with the requirements of resistance to water penetration. Contour feathers can be expected to exhibit a balance between these two opposing functions.

Our objectives were to investigate: (1) whether dippers have contour feathers similar to those of aquatic or terrestrial bird families in terms of water repellency and resistance to water penetration, and (2) if dippers that dive for their prey have a different feather structure from those that do not dive.

METHODS

Feathers from the breasts of the five species of dippers (White-throated: catalog # USNM 412413; Brown: # 582988; American: # 420411; White-capped: # 412413; Rufous-throated: # 264511) were made available through the cooperation of the Division of Birds, U.S. National Museum (USNM) at the Smithsonian Institution, Washington, D.C., USA. Only these museum specimens were used. They were examined under a Motic BA400 microscope (Motic Instruments Inc., Richmond, BC, Canada) equipped with a Jenoptik (Jenoptik AG, Jena, Germany) ProgRes® C12 digital camera to measure the diameters of the barbs ($2r$) and their separations ($2d$). Photomicrographs were made and adjusted using ProgRes® C12 (Jenoptik AG, Jena, Germany), Auto-Montage® Essentials® (Syncroscopy, Frederick, MD, USA), and Adobe® Photoshop® CS2 Version 9 (Adobe Systems Inc., San Jose, CA, USA) software.

The feathers examined were not covered by a cover slide to not distort the structure and arrangement of barbs and barbules (Rijke 1970). Parts in which the hamuli of the barbules had become unhooked and other elements that had obviously suffered from damage or abrasive effects were ignored. Only breast feathers were examined because these had been previously found to be representative of contour feathers, whereas rectrices and remiges, as a rule, do not reflect the water shedding capabilities of body feathers (Rijke et al. 1989, 2000).

At least five measurements were recorded for statistical analysis from the mid-distal section of the dorsal aspect of each feather. Five or more breast feathers from one individual of each species were measured with the total number of

TABLE 1. Barb diameters, spacing and values for $(r + d)/r$ for breast feathers of dippers compared to other groups (Rijke and Burger 1985).

		$2r$		$2d$				P_{calc} hydrostatic
	n	µm	SD	µm	SD	$(r + d)/r$	SD	m[a]
White-throated	30	24.3	0.9	149	8	7.1	0.2	0.084
Brown	51	23.6	1.0	214	9	10.1	0.2	0.060
Rufous-throated	30	23.6	0.8	160	4	7.8	0.1	0.077
American	34	24.1	0.7	186	3	8.7	0.1	0.073
White-capped	45	26.6	0.9	185	12	7.9	0.4	0.074
Starlings		34		206		7.1		0.061
Swifts		27		182		7.7		0.071
Nightjars		26		181		7.9		0.072

[a] Meters.

measurements n for each species ranging between 30 and 51. Previous work has shown that variation in barb diameter and spacing among individual birds and between males and females of each species is not statistically significant (Rijke 1970, Elowson 1984). The arithmetic mean of these measurements and their standard deviations (SD) are reported (Table 1).

RESULTS

Photomicrographs of the breast feathers of all five species of dippers are quite similar to the naked eye with barbs and barbules clearly delineated (Fig. 2). They are also similar in appearance to scanning electron microscope (SEM) micrographs of feathers of Reed Cormorant (*Phalacrocorax africanus*), Double-crested Cormorant (*P. auritus*), Brown Pelican (*Pelecanus occidentalis*), and Mallard (*Anas platyrhynchos*). Only after measuring the barb diameters and their separations did the differences in microstructure become apparent. The photomicrographs also illustrated the parallelism of the barbs in regions where barbules are normally zipped up and their divergence where the hooks and flanges of the barbules have become undone. These latter regions were discarded in our measurements.

The dimensions of the dippers' breast feathers and the pressures P, required to force water through the feather as calculated using equation 3 for $\theta = 90°$, were compared with data from earlier studies (Table 1). The barb diameter $2r$ of the five species varied little among species and was essentially the same at ~25 µm. The spacing between barbs $2d$ varied, ranging from ~149 µm for the White-throated Dipper to 214 µm for the Brown Dipper. However, no correlation was detected between the little variation in barb diameter and the larger variation in spacing. The corresponding values for $(r + d)/r$ ranged from 7.1 to 10.1. Their SD values indicate statistically significant differences between species, but with overlap for White-capped and Rufous-throated dippers (Table 1).

DISCUSSION

The values measured for $2r$, $2d$, and $(r + d)/r$ indicate that all five dipper species exhibit excellent water repellency comparable with that of typical terrestrial birds like swifts and nightjars. Spacing between the barbs in all dipper feathers studied was slightly smaller near the rachis and wider near the periphery of the feather, in agreement with previous findings for other birds (Rijke 1970). This feature is thought to increase the value of $(r + d)/r$ distally as a possible further adaptation to shedding water (Kennedy 1970, 1972).

Unfortunately, no data from studies by other authors are available in the literature. Only Elowson (1984:375), using SEM micrography, studied the feathers of one dipper species (*C. cinclus*) as part of a larger study on spread-wing postures and found that "the barbule and ramus structure was so very different from the 14 non-passerine species....that it was not possible to measure the r and d dimensions....". Elowson did not provide a SEM micrograph of this dipper specimen, but it is possible that differences in measuring technique are the source of discrepancy with the present study. This may also explain why

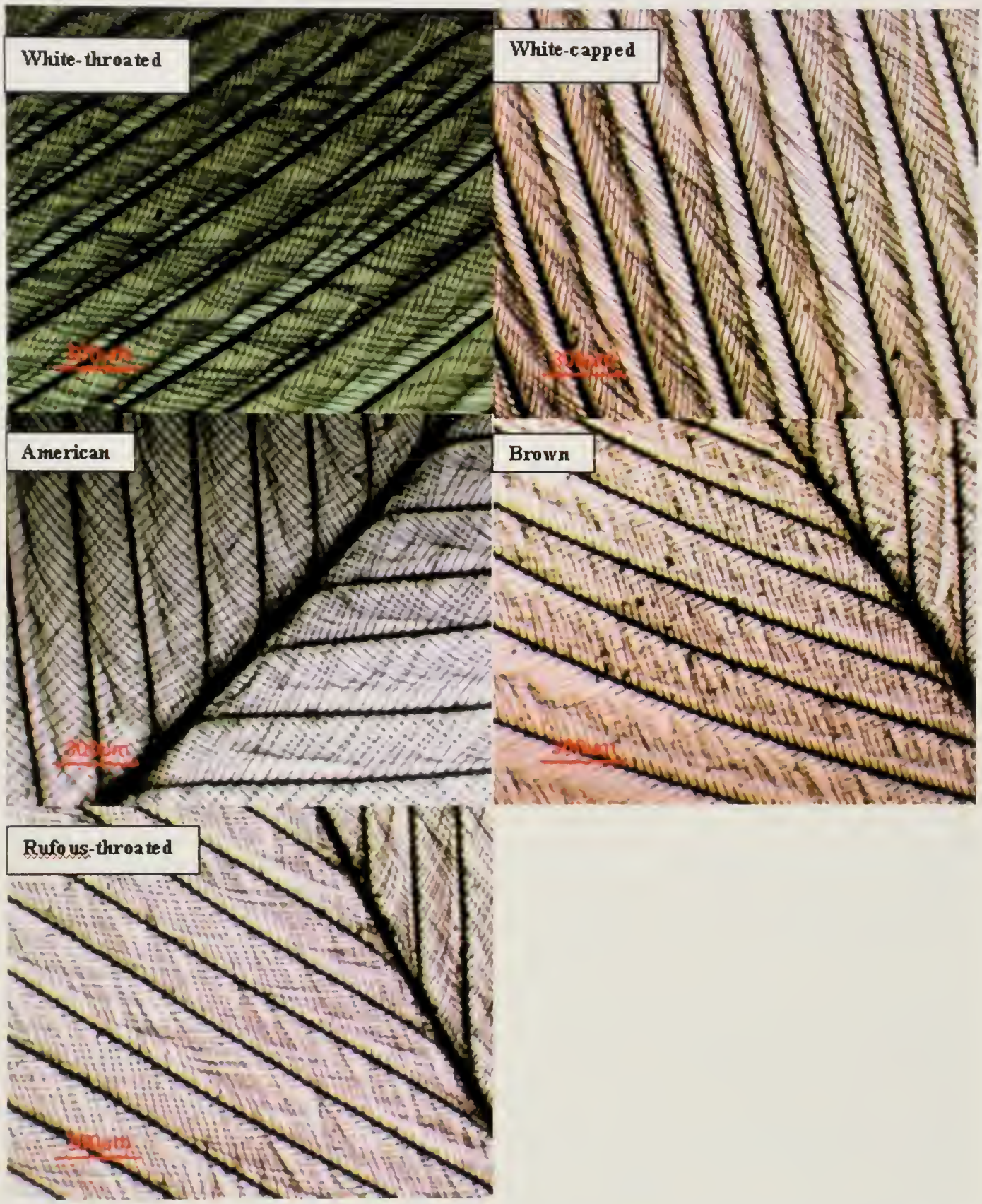

FIG. 2. Photomicrographs of the breast feathers of the five species of dippers. All micrographs are displayed at the same magnification having calibration bars of length 300 μm.

her $(r + d)/r$ value for the Mallard (~10) is very different from those of Cassie and Baxter (1944), Rutsehke (1960) and Rijke (1968), all of whom found 5.9 by transmission light microscopy.

The value for the parameter $(r + d)/r$ varied among the five dipper speeies resulting in relatively inereased resistanee to water penetration in the White-throated Dipper and increased water repelleney for Ameriean and Brown dippers (Fig. 3). The calculated values for the resistance

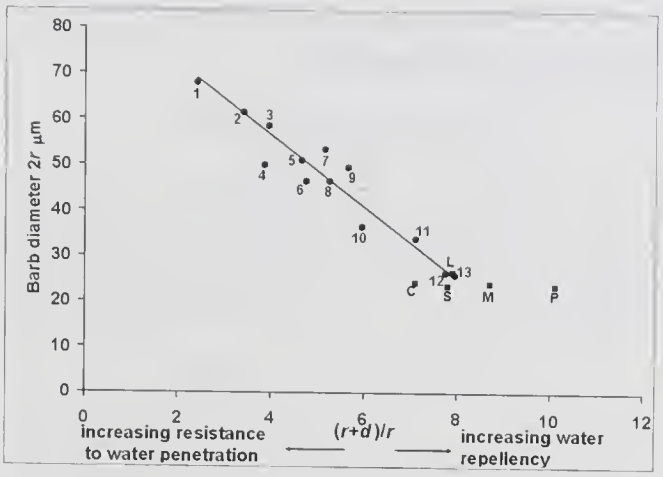

FIG. 3. Plot of averaged barb diameter $2r$ in µm against $(r + d)/r$ of the breast feathers for 18 families and species including the five species of dippers. A best-fitting straight line is drawn for the truly aquatic and truly terrestrial families (1, 2, 3, 5, 8 and 11, 12, 13) and is expressed by the equation $2r = 87.8 - 7.83(r+d)/r$. 1 = Penguins, 2 = Auks (Alcidae), 3 = Divers (Gaviidae), 4 = Gannets, 5 = Cormorant, 6 = Shearwaters, 7 = American White Pelican, 8 = Ducks, 9 = Rails, (Rallidae), 10 = Brown Pelican, 11 = Starlings, 12 = Swifts, 13 = Nightjars. Dippers: L = White-capped, C = White-throated, S = Rufous-throated, M = American, and P = Brown.

to water penetration (P_{calc}) show the inverse relationship with the r and $(r + d)/r$ values that follows directly from equation 3. They were calculated based on the diameters and spacing of the barbs of single breast feathers without considering the contributions of the barbules or the effect of stacking multiple breast feathers (Rijke et al. 1989). Thus, the actual water resistance of the entire plumage cannot be ascertained from measurements or calculations on single feathers. Therefore, the P_{calc} values shown (Table 1) serve as a relative measure among species.

There are many examples of families, and species within certain families, that have optimized the balance between water repellency and resistance to water penetration in terms of barb diameter and spacing, to suit their particular habitats and behavioral patterns (Rijke and Burger 1985). Values for $2r$ and $2d$ of breast feathers appear to depend on each other. Specifically, for truly aquatic and terrestrial families (Fig. 3), an essentially linear relationship exists between $2r$ and $(r + d)/r$ with aquatic species having wide barb diameters and small values for $(r + d)/r$, and terrestrial species having narrow barbs and large values for $(r + d)/r$. There is no apparent *a priori* reason or physical basis for this linearity. These data (Fig. 3) are useful for comparing a variety of behavioral patterns with the structural dimensions of dipper feathers, and those of typical aquatic and terrestrial families and species including families that do not obviously belong to either.

An example of the relationship between $2r$, $(r + d)/r$, and behavioral pattern is provided by the data point for gannets (Sulidae) which shows a barb diameter of 50 µm, about the same as that of cormorants (Phalacrocoracidae) and shearwaters (Procellariidae), but a smaller value for $(r + d)/r$, indicating a greater resistance to water penetration. The latter may be an adaptation to the gannet's habit of diving from the air and then pursuing prey under water. The breast feathers of Brown Pelicans have much smaller barb diameters and higher $(r + d)/r$ values than those of American White Pelicans (*Pelecanus erythrorhynchos*). The resulting increased water repellency may represent an adaptation to its habit of diving for food from the air. Brown Pelicans, unlike gannets, however, do not pursue their prey under water. American White Pelicans find their prey while swimming when resistance to water penetration will be the more important, which is reflected by the smaller values for $(r + d)/r$. Storm petrels (Hydrobatidae) with a $(r + d)/r$ of ~7.1 are another example. This high value suggests relatively poor resistance to water penetration, possibly a reason why storm petrels feed from the water surface without alighting, but when they do alight, they float buoyantly high, a condition consistent with low pressure for water penetration (Rijke and Burger 1985).

These examples suggest the specific structural dimensions of contour feathers are an evolutionary adaptation to a variety of behavioral patterns. The relatively high values for $(r + d)/r$ of dippers suggest their contour feathers, like those of truly terrestrial birds, have evolved primarily to repel water. This is reflected by typical dipper behavior: they move quickly in and out of shallow waters, rarely remain under water for >15 sec and seldom dive deeper than ~2 m. Once out of the water, a quick shake removes any remaining water drops from their feathers (Attenborough 1998).

The White-capped and the Rufous-throated dippers have contour feathers that show the same structural dimensions as contour feathers of typical terrestrial birds, whereas those of the White-throated Dipper appear to have developed a slight increase in water resistance. In contrast, the American Dipper and, in particular, the Brown Dipper with their larger $(r + d)/r$ values have

attained a substantial increase in water repellency at some expense of their water resistance. The first two species, which peck their under-water prey from a rocky perch and do not dive, show no difference in feather structure from that of truly terrestrial birds, whereas the last three are true plungers with breast feathers that show adaptations to an aquatic lifestyle. The White-throated Dipper, among these three, has evolved an adaptation to resisting water penetration; the other two have developed greater water repellency, in particular the Brown Dipper. These diverging adaptations may be explained by differences in habitat; the White-throated Dipper is more frequently found along water courses at lower altitudes, where currents are relatively slow and the water is deeper. This would favor greater resistance to water penetration. American and Brown dippers, in contrast, typically inhabit higher mountain ranges, where currents are fast and shallow, which would favor water repellency over resistance to water penetration. The geographical range of the White-throated Dipper, in its most eastern distribution, partly overlaps that of the Brown Dipper, which has probably evolved primarily in the isolation of the high Himalayan mountain ranges. Brown Dippers tend to breed at altitudes well over 5,000 m, whereas the White-throated Dipper prefers the 2,000 to 3,500 m range in Afghanistan and somewhat higher in the Himalaya. However, there is overlap in altitude, particularly at the western end of their overlapping ranges and during the non-breeding season (Ormerod and Tyler 2005).

Adaptations of dipper feathers from their terrestrial origins to their under-water feeding habits in terms of both water repellency and resistance to water penetration are consistent with our hypothesis including the observation that no similar adaptations have been made by their non-diving congeners. It is likely that plunging is a recent behavior given the dippers' passerine origins and that their feathers are primarily water repellent, and only partially adapted to either prevent water penetration or extend water repellency. Plunging is apparently, an evolutionary step that White-capped and Rufous-throated dippers have not completed.

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ANNUAL BIRD MORTALITY IN THE BITUMEN TAILINGS PONDS IN NORTHEASTERN ALBERTA, CANADA

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ABSTRACT.—Open pit bitumen extraction is capable of causing mass mortality events of resident and migratory birds. We investigated annual avian mortality in the tailings ponds of the Athabasca tar sands region, in northeastern Alberta, Canada. We analyzed three types of data: government-industry reported mortalities; empirical studies of bird deaths at tailings ponds; and rates of landing, oiling, and mortality to quantify annual bird mortality due to exposure to tailings ponds. *Ad hoc* self-reported data from industry indicate an annual mortality due to tailings pond exposure in northeastern Alberta of 65 birds. The self-reported data were internally inconsistent and appeared to underestimate actual mortality. Scientific data indicate an annual mortality in the range of 458 to 5,029 birds, which represents an unknown fraction of true mortality. Government-overseen monitoring within a statistically valid design, standardized across all facilities, is needed. Systematic monitoring and accurate, timely reporting would provide data useful to all concerned with bird conservation and management in the tar sands region. *Received 17 November 2009. Accepted 5 May 2010.*

Global demand for unconventional energy sources such as coal bed methane, heavy oil, and bitumen has grown in recent years. Bitumen in northern Alberta, Canada, is extracted by two methods, *in situ* well-based approaches and truck and shovel open pit mining. The latter method produces ''tails'' during separation of bitumen from the sand. The tails, a mixture of process-affected water, residual hydrocarbons, brine, silts and clays, and metals are discharged into tailings ponds. The extent of tailings ponds in northeastern Alberta grew by 422% between 1992 and 2008 (Timoney and Lee 2009). The Athabasca tar sands development is one of the largest energy projects in the world. Production of bitumen is predicted to rise from the current 1.3 million barrels/day to three million barrels/day by 2018 (Alberta Energy 2009).

Water bodies along migration routes attract many bird species as they afford foraging, roosting, nesting, and resting opportunities (Ronconi 2006). A variety of deterrents have been used to discourage waterbirds from landing in tailings ponds such as floating and beach effigies, propane scare cannons, and sound-producing systems (Boag and Lewin 1980, Golder Associates Ltd. 2000, Ronconi and St. Clair 2006). Some birds that land at tailings ponds become oiled and a proportion of the oiled birds later die. Bird mortality rates from oiling have not been precisely measured, but casualties appear to be high for gregarious species, particularly for diving birds (Clark 1984). Bird migration is affected by weather as birds are more likely to land when they encounter headwinds, low temperatures, and precipitation (Newton 2007). Storms may increase the likelihood of bird oiling at tailings ponds (Ronconi 2006), and inclement weather may increase the probability of mass mortality events.

Oiled ducks may suffer from reduced insulation, increased metabolic rate, and hypothermia even from small amounts of oil (Hartung 1967, McEwan and Koelink 1973). Survival rates of rehabilitated birds may be as low as 1 to 20% for some species (Mead 1997). Birds from 43 species have died due to exposure to tailings ponds in the area, mostly waterbirds such as dabblers and divers: Mallard (*Anas platyrhynchos*), Common Goldeneye (*Bucephala clangula*), Northern Shoveler (*Anas clypeata*), Lesser Scaup (*Aythya affinis*), American Coot (*Fulica americana*), grebes, mergansers, geese, and shorebirds including Semipalmated Sandpiper (*Calidris pusilla*), Pectoral Sandpiper (*C. melanotos*), Stilt Sandpiper (*C. himantopus*), and Lesser and Greater Yellowlegs (*Tringa flavipes, T. melanoleuca*) (Sharp et al. 1975, Dyke et al. 1976, Gulley 1980, Ronconi 2006). Deaths of birds of prey, gulls, passerines, and other groups have also been documented. Mortality rates may be high even at small ponds: 27 dead birds were found at a 0.4-ha tailings pond lacking deterrents (Dyke et al. 1976). There may be continual ''incidental take'' of birds during the open water season, especially at night when human observations are impractical. Oiled birds in tailings ponds have been observed to sink out of

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sight (Dyke et al. 1976), minimizing the chance of detection.

Our objective was to provide estimates of annual bird mortality resulting from bitumen tailings pond exposure in northeastern Alberta, Canada through synthesis and analysis of available data. These data included numbers reported by industry to government and scientific data on mortality and landing rates at tailings ponds.

METHODS

Study Area.—We studied avian mortality in the Athabasca bitumen (tar) sands region (geographic center at 57° 03′ N, 111° 31′ W, Fig. 1) in the lower Athabasca River watershed north of the city of Fort McMurray, Alberta, Canada. The 120.6 km^2 of tailings ponds within the area of open pit mining, as of March 2008, covered 1.4 times the area of natural water bodies (84.9 km^2) composed of the surface of the Athabasca River (50.4 km^2) and lakes, ponds, and other river surfaces (34.5 km^2) (Timoney and Lee 2009; KPT and RAR, unpubl. data). The area lies within a convergence zone of North American waterfowl flyways; millions of birds migrate through northeastern Alberta *en route* to and from local and distant breeding areas in northern Alberta, the Peace-Athabasca Delta, Mackenzie River Valley, and the arctic (Butterworth et al. 2002, Thomas 2002, USDI 2009b). Thirty-five species and species groups of waterbirds, and 29 other species have been observed on one lease (Syncrude # 17) at the natural water body Mildred Lake (Sharp et al. 1975). More than 16,000 birds were observed flying over one tailings pond during spring migration (Ronconi and St. Clair 2006) while more than 25,000 swans, geese, ducks, Sandhill Cranes (*Grus canadensis*), and gulls were observed in daylight during a fall migration at Syncrude Lease # 17 (McLaren and McLaren 1985). The total number of migratory birds passing through the lower Athabasca River Valley is unknown.

Data Collection and Analyses.—Spot censuses and shoreline searches for dead birds of varying duration, extent, and frequency at tailings ponds of known areal extent during the open-water season (Gulley 1980, Van Meer and Arner 1985) were used to calculate bird mortalities per km^2 from which mortalities were adjusted to the 2008 areal extent of tailings ponds. Mortality data were collated from three companies with tailings ponds (Suncor 1990–2008, Syncrude 2000–2007, and Shell Albian 2000–2008). Data were obtained from reports produced by the companies (Syncrude 2008), and from the Alberta government (Sustainable Resources Development) under a freedom of information request (K. P. Timoney, October 2008). These data, reported by company, year, and mortality type were analyzed to obtain mean annual mortality. We estimated the total number of birds landing and subjected to oiling during spring migration at the Albian Sands Muskeg River Mine: landings/hr (from Ronconi and St. Clair 2006) and oiled birds/day (from Ronconi 2006).

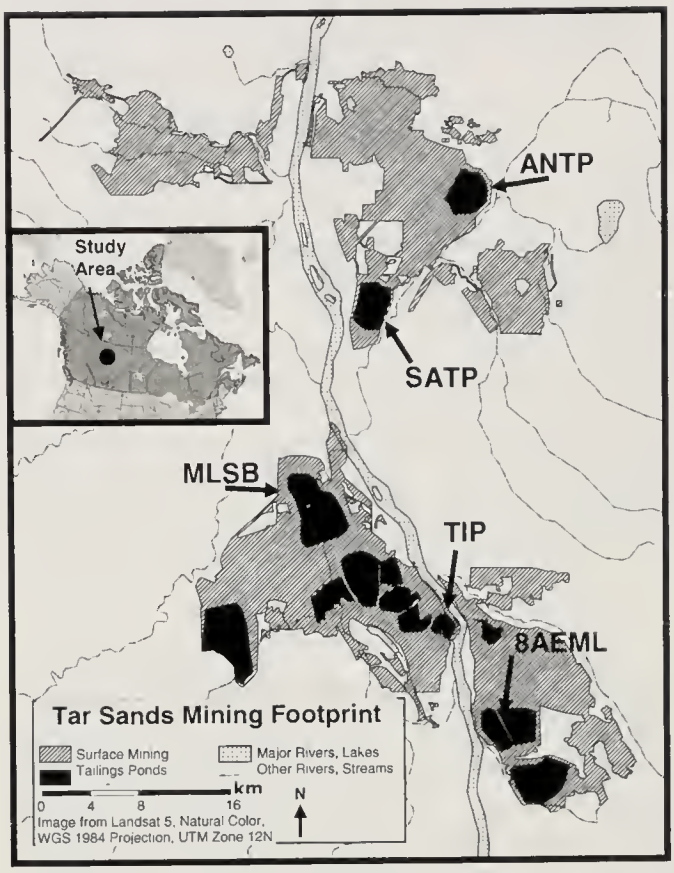

FIG. 1. Study area (modified from Timoney and Lee 2009). Areas (as of 19 March 2008) undergoing bitumen extraction are hachured; tailings ponds are black. Tailings pond names are MLSB = Mildred Lake Settling Basin; ANTP = Aurora North tailings pond; SATP = Shell Albian tailings pond; TIP = Tar Island Ponds 1 and 1A; 8AEML = Suncor Millennium tailings ponds 8A and EML.

RESULTS

Mortality Rates Estimated by Systematic Surveys.—Systematic surveys for dead birds at tailings ponds (Table 1), used to calculate mortality per km^2 (range 7.2 to 145.2 birds), were extrapolated to estimate total potential mortality based on 120.6 km^2 of tailings ponds in 2008. An estimate based on the lowest observed mortality at

TABLE 1. Estimated annual bird mortality/km²/year in the Athabasca tar sands tailings ponds based on spot counts and systematic shoreline surveys.

Site	Area (km²)[a]	Year	Dead birds	Dead birds/km²	Reference[c]	Comments
MLSB	12.25	1984	94	7.68	1, 3	scare cannons, human effigies
MLSB	11.74	1985	84	7.15	1, 3	scare cannons, human effigies
MLSB	11.58	1980–1983[b]	189.5	16.36	1, 3	scare cannons, human effigies
Pond 1	1.86	1977	77	41.40	2	human effigies; fresh tailings received 95% of days (Apr–Oct)
Pond 1	1.86	1978	79	42.47	2	human effigies; fresh tailings received 100% of days (Apr–Oct)
Pond 1	1.86	1979	270	145.16	2	human effigies with artificial lighting at night; fresh tailings received 92% of days (Apr–Oct)
Pond 1A	0.56	1977	43	76.79	2	deterrents?[d]; fresh tailings received 34% of days (Apr–Oct)
Pond 1A	0.56	1978	31	55.36	2	deterrents?[d]; fresh tailings received 25% of days (Apr–Oct)
Pond 1A	0.56	1979	33	58.93	2	deterrents?[d]; fresh tailings received 0% of days (Apr–Oct)

[a] Areas of MLSB derived from planimetry of airphotographs (1980, AS2165-13; 1984, AS3051-5; 1986, AS3356-280; Ponds 1 and 1A areas derived from Gulley (1980).

[b] Dead birds/year 1980–1983 derived mathematically from reported values for 1984 and 1980–1984 (Van Meer and Arner 1985): 1980–1984 average mortality of 170.4 birds/year; total birds dying 1980–1984 = 170.4 × 5 = 852 birds; 1984 mortality of 94 birds; 1980–1983 average mortality = (852 − 94)/4 = 189.5 birds/year, or 16.36 birds/km²; the average weighted mean mortality 1980–1985 = ((16.36 × 4) + 7.68 + 7.15)/6 = 13.38 birds/km². The high estimate of annual mortality is the weighted mean mortality per km²; it is the sum of 500.38 birds/km² for 12 years of data (1980–1983 comprises 4 years of data), 500.38/12 = 41.70 birds/km².

[c] References: 1 = Van Meer and Arner (1985); 2 = Gulley (1980); 3 = Golder Associates Ltd. (2000).

[d] Queries sent to Suncor (17 Nov to 12 Dec 2008) regarding deterrents in use on Pond 1A during 1977–1979; no reply received to date (4 May 2010).

Syncrude's Mildred Lake Settling Basin (MLSB) of 7.2 birds/km² in 1985 yielded an annual mortality of 863 birds. A medium estimate based on Syncrude's MLSB (1980–1985) average mortality of 13.38 birds/km² yielded an annual mortality of 1,614 birds. A high estimate based on the weighted mean mortality rate for all years at Syncrude's MLSB and Suncor's Tar Island Ponds 1 and 1A of 41.7 birds/km² yielded an annual mortality of 5,029 birds.

Industry-based Annual Mortality Reported to Government.—Annual mortality attributed to oiling over the period 2000 to 2007 ranged from 17 to 201 birds. The weighted mean (± SD) annual mortality was 65 ± 59 birds. (Table 2). Additional annual mortalities attributed to 'other' and to 'unknown' causes (details in Table 2) averaged (± SD) 13 ± 9 (max 31 in 2007) and 16 ± 9 birds, respectively. Industry data had poor agreement with the government data released under the freedom of information request (Table 3); the mean difference was 19%.

Annual Bird Mortality Estimated by Landing and Oiling Rates.—A spring landing rate of 121.44 birds/day in a 3.5 km² tailings pond was calculated, resulting in an estimated rate of 34.69 landings/km²/day during daylight hours only (low estimate, Table 4). We calculated 54.93 landings/day (109.86 landings/km²/day) (high estimate, Table 4) from observations at a 0.50-km² area where deterrent testing occurred (RAR, unpubl. data not previously reported in Ronconi and St. Clair 2006). Scaling for the total area of tailings ponds in 2008, about 125,513 to 397,408 birds may land during a 30-day spring migration period. Thirteen oiled waterbirds and shorebirds were found during the same period and at the same site (Ronconi 2006), most of which were covered in >50% oil, from which oilings/day and the proportion of landed birds becoming oiled were calculated (Table 4). We estimate that 286 to 905 birds may be oiled during spring migration at an overall oiling rate of 0.2278% for birds that landed on ponds. About 229 to 815 birds may die each spring due to oiling if an oiled bird is unable to land more than once, and 80 to 90% of oiled birds die (Discussion).

DISCUSSION

Uncertainties in Mortality Estimates.—Bird oilings may peak in August and September rather than in spring (Van Meer and Arner 1985), and it is reasonable to double the spring mortality to derive an annual mortality of ~458 to 1,630 birds.

TABLE 2. Bird mortalities attributed to oiling, 'other' and 'unknown' causes released by the Alberta Government for petroleum companies with tailings ponds in northeastern Alberta.[a]

	Oiling[b]			Other			Unknown		
Year	Suncor	Syncrude	Albian[b]	Suncor	Syncrude	Albian	Suncor	Syncrude	Albian
1990	103			0			0		
1991	93			0			0		
1992	194			0			2		
1993	135			0			4		
1994	87			0			1		
1995	43			0			0		
1996	72			0			4		
1997	71			0			6		
1998	80			0			3		
1999	48			0			10		
2000	193	8		0	2	1	12	7	0
2001	2	15		0	2	0	23	3	0
2002	17	20		1	6	3	1	2	1
2003	15	16	17	2	23	3	2	5	0
2004	10	33	2	0	5	2	2	9	1
2005	3	8	14	2	18	2	1	16	1
2006	3	57	3	4	8	7	3	8	4
2007	9	10	26	1	7	6	6	19	6
2008[c]	16		4	0	2	1	0	2	4
Recent Mean ± SD[b]	31.5 ± 65.5	20.9 ± 16.7	12.4 ± 10.0	1.2 ± 1.4	8.9 ± 7.6	3.0 ± 2.4	6.2 ± 7.7	8.6 ± 6.0	1.6 ± 2.2

[a] 'Other' includes electrocution, collisions, predation, fights with other birds, and natural causes; 'Unknown' includes incidents where company was not able to identify cause of death and incidents where cause of death was not reported.

[b] Tailings pond at Shell Albian began to fill in 2003; mortality due to oiling not expected prior to 2003. Calculations of recent tailings pond mortalities used years 2000–2007 for Suncor and Syncrude and years 2003–2007 for Shell Albian. Mortality means for 'other' and 'unknown' use the period 2000–2007. Mortality means are for each company and mortality type. Average mortalities by year, 2000–2007, oiling 64.8 ± 58.7, other 13.1 ± 9.3, and unknown 16.5 ± 9.1.

[c] Values for 2008 were 'year to date' current to July 2008 with the exception of Syncrude for which the death of 1,606 ducks at the Aurora North tailings pond in April 2008 was not made public until 2009.

This adjustment to the mortality estimate may be conservative as it does not include mortalities that occur before spring, between spring and fall migration, and after fall migration. Annual tailings pond mortality estimates derived from mortality surveys (863 to 5,029 birds) and landing-oiling rates (458 to 1,630 birds) are roughly of the same magnitude. Self-reported oiling mortality data from industry provide the lowest estimate (65 bird deaths/year) whereas Wells et al. (2008) provide a high estimate of 8,676 to 156,168 bird deaths/year. Wells et al. (2008) assumed that all birds that land at tailings ponds are oiled and that peak landing rates exist 24 hrs/day for 100 days. Our mortality estimates may be conservative given that 500,000 to one million birds die annually at oilfield wastewater ponds in the United States (USDI 2009a). Those wastewater ponds are similar to bitumen tailings ponds in their mixture of water, residual oil or bitumen, and salts.

The presence of extensive tailings ponds

TABLE 3. Annual bird mortality at Syncrude[a] as reported by the Alberta government and by Syncrude (2008).

	Year							
Source	2000	2001	2002	2003	2004	2005	2006	2007
Alberta Government	17	20	28	44	47	42	73	36
Syncrude	20	21	31	44	69	55	46	35
Difference[b], %	−18	−5	−11	0	−47	−31	37	3

[a] Combined Mildred Lake and Aurora leases.

[b] Difference = (Government − Syncrude/Government) × 100; mean difference without regard to sign = 19%.

TABLE 4. Rates of landing and the proportion of birds that subsequently become oiled at Shell Albian Sands tailings pond during April–May 2003.[a]

	Number of birds landing	Landings/hr	Landings/day[c]	Oiled birds	Oilings/day	% Landed birds that became oiled
Ducks	536	3.99	63.69	7	0.149	0.23
Shorebirds	444	3.30	52.76	4	0.085	0.16
Geese/Swans	10	0.07	1.19	1	0.021	1.79
Gulls	13	0.10	1.54	1	0.021	1.38
Other waterbirds [b]	19	0.14	2.26	0	0.000	0.00
Overall	1,022	7.60	121.44	13	0.277	0.23

[a] Data compiled from spring migration studies in the 3.5 km^2 main tailings pond at Shell Albian Sands, Muskeg River Mine (Ronconi 2006, Ronconi and St. Clair 2006) yielding a low estimate of 34.69 landings/km^2/day; there were 54.93 landings/day within the 0.50 km^2 observation area yielding a high estimate of 109.86 landings/km^2/day; 47 days of observation for oiled birds.

[b] Loons, grebes, cranes, herons, cormorants, and coots.

[c] Observations for daylight hours only; average 15.97 hrs of daylight between 18 April and 29 May, 134.4 hrs of observation (source: www.almanac.com/rise for Fort McMurray, AB, Canada).

containing bitumen, polycyclic aromatic hydrocarbons (PAHs), naphthenic acids, brine, heavy metals, and ammonia along an internationally significant migratory bird corridor poses long-term threats to migratory and resident birds (Schick and Ambrock 1974, Wells et al. 2008). Tailings ponds may pose the greatest threat in spring when warm effluent-fed tailings ponds provide open water at a time when natural water bodies remain frozen; however, a high risk of oiling may extend throughout the open water season (Van Meer and Arner 1985).

There are four aspects of our estimates that influence their accuracy. First, no nocturnal observations of migrating or landing birds were made. Many birds migrate at night (Richardson 1971, Blokpoel 1973, Blokpoel and Burton 1973), but landing rates during darkness are unknown. Many birds migrate at night and mortality rates might be higher if data from night-time observations were available. There are also no observations for November through early April, when natural water bodies are frozen but large areas of tailings ponds remain unfrozen due to addition of warm tailings. The frequency of landings then is unknown, but is presumably greater than zero for resident birds. Higher rates of nocturnal landings and landings in non-migratory periods would increase our estimates.

A second source of estimation error is that numbers of birds flying over, landing, becoming oiled, or being found dead are an unknown fraction of the true parameter values. Some of these parameters were estimated from the most recent and systematically collected data available (e.g., Ronconi 2006, Ronconi and St. Clair 2006); however, without data from other sites and years, there is no means to assess variation in rates of birds landing, becoming oiled, or dying.

Third, we assumed a mortality rate of 80 to 90% for birds that came in contact with oil. Mortality rates of oiled birds are unknown (Clark 1984), but even very small amounts of oil may kill birds (Hartung 1967, McEwan and Koelink 1973) and survival rates of rehabilitated oiled birds may be as low as 1 to 20% (Mead 1997). Our estimates assume a small proportion (10–20%) of oiled birds may survive oiling.

Finally, by scaling our estimates from individual tailings ponds to the areal extent of tailings ponds in the region, we assumed that bird use and associated mortalities are similar across sites. This assumption remains untested and, for some species such as shorebirds, the extent of shoreline contaminated with bitumen may be a better predictor of mortality than extent of open water.

Individual events may result in large variations in mortality. A migratory waterfowl mortality event at the Syncrude Aurora North tailings pond occurred in April 2008 at which 1,606 dead waterfowl were later found (CBC 2008, 2010). Provided that all dead waterfowl were found and no non-waterfowl died, the single event resulted in a mortality of 162 birds/km^2 well in excess of our highest estimate (Table 1). The frequency of mass mortality events is unknown.

Inconsistencies and Deficiencies in Reporting Bird Mortality.—We note three major shortcomings in the data provided by government and industry. First, mortality estimates based on mortality surveys and landing/oiling rates are far higher than those reported by government. Second, industry-reported mortalities often do not match mortalities reported by the government

(Table 3), even though government and industry numbers should be identical. Third, the bird mortality data released by government lack detail. Only company name and total bird mortality for each year and general cause of death are reported; this results in loss of valuable data on location, date, and circumstances of specific incidents.

Sampling design, including appropriate sample size, sampling effort, and accurate detection and identification of species is a critical aspect of an effective monitoring protocol (McComb et al. 2010). Numbers of bird mortalities are directly related to search effort and sampling design. Industry-reported data on bird deaths are problematic as they are not systematic, repeatable, and statistically robust. Review of mortality data in Syncrude annual reports indicates that few of the observations come from tailings ponds, which is likely where most oiled birds die. Syncrude (2006, 2008) reported underestimating mortality when explaining an increasing trend in bird mortality in recent years as partially attributable to improved monitoring and reporting practices.

The Need for Improved Data.—Currently, neither the total number of birds migrating through the region nor the total annual bird mortality attributable to tailings ponds are known with sufficient scientific rigor. Data on mortalities during extreme weather events are lacking. The fate of lightly-oiled birds that continue migration, in particular to summer breeding areas, is unknown. Important questions remain about the variability in landing and oiling probability with season, weather conditions, time of day, and pond size and location. Questions also remain about mortality detection efficiency in relation to sampling effort, monitoring protocols, and tailings pond size. The *ad hoc* monitoring by industry, sanctioned by government, is inconsistent, cannot answer these questions, and undoubtedly underestimates actual mortality.

CONSERVATION IMPLICATIONS

The pace and scale of development of the Athabasca tar sands is unprecedented in North American history. The industrial footprint and resultant habitat loss may double in 15 years and will certainly increase bird mortality rates. Open pit bitumen extraction may exert population-level impacts upon migratory and resident birds, and is capable of causing mass mortality events. Existing natural water bodies should be protected to help offset landings of birds in tailings ponds (Ronconi 2006). Production of liquid tailings should be phased-out before this expansion of the industry occurs.

Tailings ponds exceed the extent of natural water bodies in the area, continue to increase in extent, and lie along an internationally significant flyway; thus, they may pose a significant regional mortality risk. Harmful effects of tailings ponds are not limited to oiling of waterbirds. Ingestion of bitumen grit by waterfowl may be a significant route of exposure to contaminants (King and Bendell-Young 2000). Nesting Tree Swallows (*Tachycineta bicolor*) exposed to process-affected wetlands have higher mortality, hormonal stress, nestling parasitism, and reduced nesting success (Wayland and Smits 2004, Gentes 2006). The effects were attributed to PAH exposure, possibly through feeding on contaminated insects.

A variety of strategies have been tested to reduce the attraction of birds to industrial developments (Brough and Bridgman 1980, Stevens and Clark 1997, Read 1999; and reviews by Bomford and O'Brien 1990, Donato et al. 2007). The tar sands industry in northeastern Alberta has been using landing deterrents such as propane cannons and scarecrows for >30 years (Boag and Lewin 1980, Gulley 1980, Golder Associates Ltd. 2000). One of the long-standing problems of bird deterrents is habituation (Bomford and O'Brien 1990, Stickley et al. 1995, Conover 2001). A recent comparison of modern deterrent techniques found the odds of landing at "protected" bitumen tailings ponds remained high relative to non-deterrent controls (Ronconi and St. Clair 2006). Overall, these authors observed no significant difference in the deterrence value of industry standard versus radar-activated systems. The effectiveness of existing deterrents may be enhanced with development of compensation ponds (Read 1999, Donato et al. 2007), providing clean water and a positive stimulus for birds deterred from tailings ponds.

Government should assume responsibility for development of systematic monitoring and research on tailings pond bird landing, oiling, and mortality rates. The work should be conducted by independent scientists using a statistically valid sampling design with emphasis on spring and fall migration. A rigorous and systematic monitoring plan standardized across all facilities is likely to yield a better understanding of the factors contributing to avian mortality at tailings ponds than *ad hoc* monitoring. These data would be

valuable to development and refinement of effective mitigation strategies (e.g., deterrents and compensation ponds) as a component of an adaptive management approach towards reducing avian mortalities. Well-designed monitoring programs help managers and policy makers to reach informed decisions based on facts (McComb et al. 2010). Systematic monitoring and accurate, timely reporting would provide data useful to all concerned with bird conservation and management in the tar sands region.

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ABUNDANCE AND DISTRIBUTION OF WATERBIRDS IN THE LLANOS OF VENEZUELA

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ABSTRACT.—The Llanos is a significant waterbird site in the Western Hemisphere, but abundance and distribution of waterbirds across this vast region are poorly known, which hampers conservation initiatives. We used point counts along road routes in the Llanos region of Venezuela to examine abundance and distribution of waterbirds during 2000–2002 within five ecoregions across the Llanos. We detected 69 species of waterbirds and recorded 283,566 individuals, of which 10 species accounted for 80% of our observations. Wading birds (Ciconiiformes) represented the largest guild both in numbers of species (26) and individuals (55%), followed by waterfowl (26%), and shorebirds (11%). Five species comprised 62% of all individuals: Cattle Egret (*Bubulcus ibis*), White-faced Whistling Duck (*Dendrocygna viduata*), Black-bellied Whistling Duck (*D. autumnalis*), Great Egret (*Ardea alba*), and Wattled Jacana (*Jacana jacana*). Wading birds were particularly ubiquitous with at least 21 of 26 species recorded in each of the ecoregions. Species richness (66), proportion of waterbirds detected (54%), and mean number of birds per route (1,459) were highest in the Banco-Bajio-Estero savanna ecoregion. Our study provides the most comprehensive data set available on waterbirds in the Llanos of Venezuela and highlights regions of special conservation concern. *Received 20 April 2009. Accepted 7 October 2009.*

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Erratum

The second author's name was inadvertently left off of the article published in the March 2010 Issue (Volume 122: 102–115). We apologize for this error. The corrected author sequence is shown above.

Short Communications

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Piping Plover Foraging Distribution and Prey Abundance in the Pre-laying Period

Jonathan B. Cohen[1,2] and James D. Fraser[1]

ABSTRACT.—Migratory birds arriving in breeding areas should select territories that maximize reproduction and survival. Prey available prior to egg laying may be as important as prey availability for chicks later in the season. We sampled benthic and terrestrial prey items in Piping Plover (*Charadrius melodus*) foraging habitat soon after they arrived in breeding areas in New York during 2001–2003. Benthic invertebrates in the sand flats were abundant and available to adults, whereas terrestrial arthropods typically used later in the season were sparse in all cover types. Foraging adults selected intertidal sand flats over other microhabitats. One benefit of nesting near sand flats apparently is abundant food upon arrival in breeding areas. Protecting habitat between arrival in breeding areas and territory establishment is uncommon but warranted for this threatened species. *Received 4 September 2009. Accepted 17 March 2010.*

Choice of a breeding territory is a key determinant of avian fitness and is made based on proximate cues that, in good habitat, will be correlated with fitness benefits (Fretwell and Lucas 1970). These cues may be related to cover from predators (Benson et al. 2009), intraspecific social attraction (Harrison et al. 2009), nest site availability (Rhodes et al. 2009), and food availability (Earnst and Rothe 2004). Food abundance during egg-laying may be critical both to current and future avian reproductive success via effects on adult energy reserves (Martin 1987). Lack (1954) proposed that breeding should be timed so chicks should hatch at the time of greatest food abundance. However, habitat quality during territory establishment (i.e., between the start of the breeding season and egg-laying) and during brood-rearing may not be correlated (Nooker et al. 2005). Thus, adults cannot forecast availability of food for chicks by prey abundance leading up to and during egg-laying (Kirstan et al. 2007).

Selecting habitat that does not provide adequate food for chicks is not a viable strategy, but food availability for the young may not necessarily be a proximate cue for decisions about territory location and size. Prey used by adults and chicks during the breeding season may be entirely different for some bird species, (Wilson et al. 2004) or partially overlap (Shealer 1998, Jiguet 2002). Diets of adult and chick Eurasian Dotterels (*Charadrius morinellus*) differed early in the breeding season and became more similar as soft-bodied prey became more prevalent (Galbraith et al. 1993).

Precocial birds may benefit more than altricial species from settlement decisions based on habitat conditions at time of territory establishment, rather than on a forecast of future conditions, because they can move their broods to high-quality foraging habitat soon after hatch (Kosztolanyi et al. 2007). Our objective was to examine the types and distribution of prey available to Piping Plover (*Charadrius melodus*) adults upon arrival in breeding areas. Foraging adults tend to concentrate in intertidal flats upon arrival at East Coast breeding sites where those habitat features are available (Fraser et al. 2005), whereas after the breeding season chicks forage in a range of upland and intertidal habitats (Elias et al. 2000). We predicted that intertidal flats would provide abundant prey between arrival and egg-laying.

METHODS

Our study area was West Hampton Dunes, New York, USA (40 46.5′ N, 72 43′ W) from 2001 to 2003. This 2.8-km long barrier island village was 200–500 m wide, bounded by the Atlantic Ocean to the south and Moriches Bay to the north. The ocean shoreline of the island was characterized by a relatively linear high-wave energy intertidal zone with fresh wrack (washed-up organic debris) at the daily high tide line. The bay shoreline of the island was a low-wave energy intertidal zone, including portions of linear shoreline interrupted

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by 27 ha of irregularly shaped sand flats with fresh wrack at the daily high tide line.

Piping Plover adults arriving to breed on the Atlantic Coast forage primarily on intertidal sand flats and mudflats that may or may not be contiguous with sandy beaches used for nesting (Cairns 1982, Fraser et al. 2005). Nesting pair density is higher at sites that contain sand flats adjacent to nesting areas than at sites that do not (Patterson et al. 1991, Elias et al. 2000, Cohen et al. 2009), suggesting a fitness benefit of nesting near sand flats. Adults forage on benthic polychaetes and crustaceans (Cairns 1977) and terrestrial arthropods (Shaffer and Laporte 1994). Adults lead chicks to foraging sites after the eggs hatch where they prey primarily on adult arthropods (Cuthbert et al. 1999); chicks generally do not prey on benthic invertebrates until they are near fledging. Sand flats provide abundant arthropods in summer (Cohen et al. 2009), but nesting Piping Plovers arrive before insects typically emerge. Thus, prey for chicks cannot be a proximate influence on territory selection.

We collected 10-cm diameter × 2-cm deep sediment cores from randomly-selected sites from the bay side intertidal flats using sections of PVC pipe. We collected all samples on 1 day, within a week of the first large arrival of Piping Plovers. Piping Plovers forage on invertebrates at or just under the surface, and our cores represented the zone with the most readily available prey. Sediment samples were stored in 1-L Nalgene jars filled with 100% ethanol. We later sorted organisms from the sediment samples and counted them by general category (polychaete worms, crustaceans, insect larvae, and other organisms).

We sampled adult arthropods in several cover types on the ocean and bay side of the island using paint stirrers coated, except for the handles, with Tanglefoot Insect Trap Coating (The Tanglefoot Company, Grand Rapids, MI, USA). These cover types included intertidal zone (the zone between the water and the day's high tide line, which on the bay side contained the sand flats), fresh wrack (washed up organic debris from the most recent high tide), old wrack (clumps of sand-covered wrack deposited by earlier high tides), backshore (flat, dry sandy area between the mean high tide line and the dune, including bare and vegetated substrates), and dune (a low sandy ridge). We placed one pair of paint stirrers in each cover type on each of six transects, the first of which was placed at random within 100 m of the edge of the site and the rest were evenly-spaced at 420-m intervals. We placed one stirrer vertically in the sand with the uncoated handle buried and the flat surface facing the water's edge. The other stirrer was horizontal on the ground 10 cm south of the vertical stick with its long axis parallel to the water's edge. The area exposed was 64.5 cm^2 (21.5 × 3 cm) for the horizontal stick (coated on the upper side only) and 129 cm^2 for the vertical stick (coated on both sides, Loegering and Fraser 1995). We collected sticky trap samples in 1 day within 1 week of collecting sediment samples. The sticks were exposed for 3 hrs between mid-falling and mid-rising tide, starting between 0700 and 1000 hrs, after which we recorded the number of arthropods in different taxa.

We performed a census of Piping Plovers in the study area concurrent with arthropod sampling, and recorded the numbers that were foraging in 2002 and 2003. We calculated the proportion of birds in each cover type on the bay and ocean side of the island, including upland and intertidal areas. We also measured the area of the intertidal zones and upland zones (the aggregation of non-intertidal cover types) from aerial photographs taken before 5 May each year by tracing polygons on digitized versions of the photographs in ArcView 3.1 (ESRI, Redlands, CA, USA). We then calculated the percent area of those cover types.

RESULTS

We observed the first Piping Plovers at the site between 12 and15 March with larger numbers (~ 20) arriving between 18 and 21 March. The earliest recorded nest at the site was on 17 April.

We found low numbers of terrestrial arthropods, and many sticky traps caught no arthropods (Table 1). By contrast, there were abundant benthic invertebrates in the bayside intertidal zone (Table 1). No sediment cores were totally devoid of organisms. The benthos in the cores comprised mainly polychaete worms, crustaceans, and insect larvae with the proportions of each depending on year (Fig. 1).

We observed 93 ± 1% ($\bar{x}$ ± SE) (n = 46) of foraging Piping Plovers in the bay intertidal zone in 2002, which comprised 32% of the habitat area. The other 7 ± 1% were using the ocean intertidal zone which comprised 8% of the habitat area. The remaining 60% of the area was unused upland. We only observed seven foraging Piping Plovers

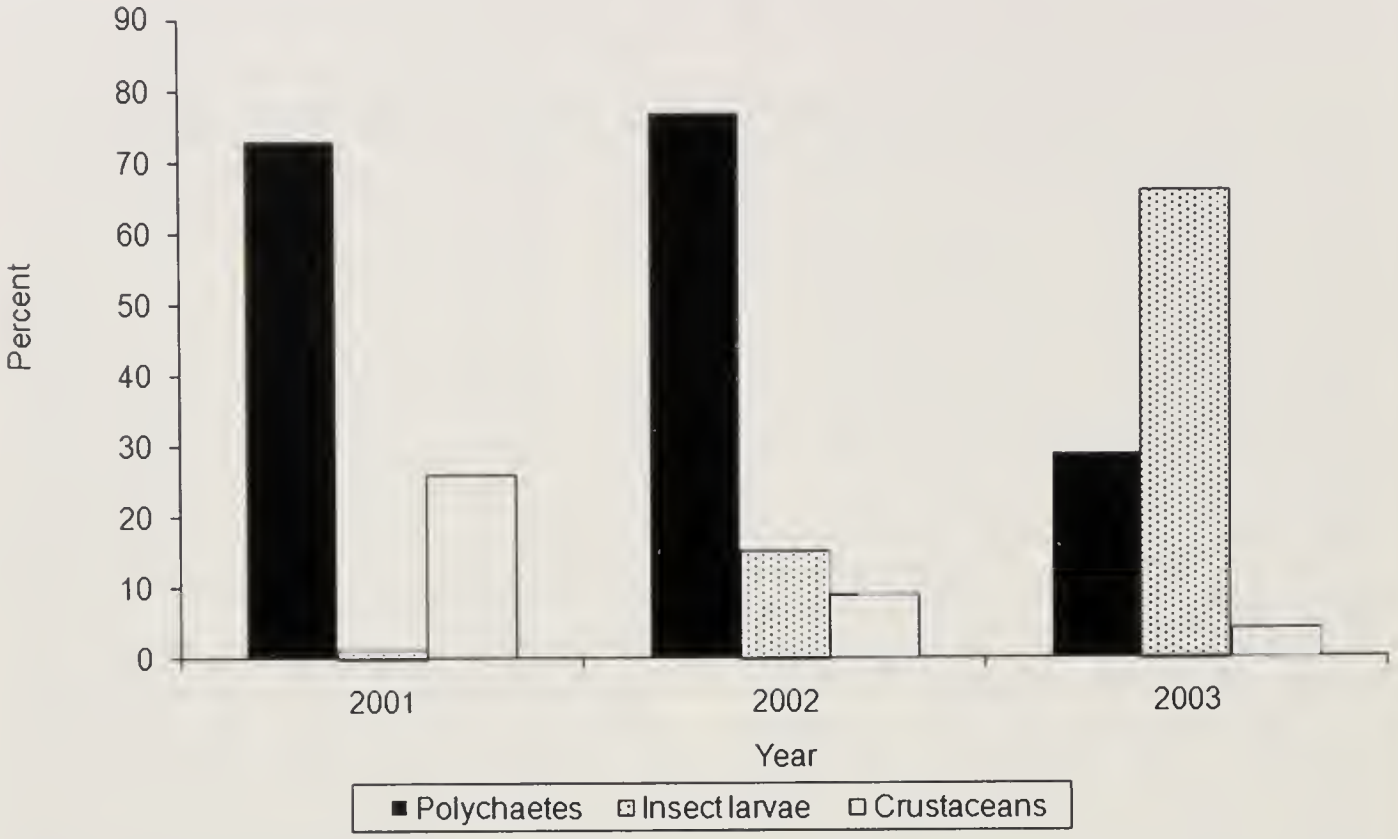

FIG. 1. Mean percent abundance of polychaete worms, insect larvae, and crustaceans in benthic cores from intertidal sand flats in a Piping Plover breeding area, West Hampton Dunes, New York, 2001–2003.

in 2003, all of which were in the bay intertidal zone, which comprised 38% of the habitat area.

DISCUSSION

The prey base when Piping Plovers arrived in breeding areas largely consisted of intertidal zone benthos. We did not have the resources to sample and analyze the ocean intertidal zone benthos, but in casual observations we noted Piping Plovers foraging on worms there. The plovers were distributed between two habitats (sand flats and ocean intertidal zone) that provided benthic prey. The substrate in upland areas was dry sand and

TABLE 1. Prey organisms in Piping Plover foraging habitat, caught in terrestrial sticky trap samples and benthic core samples, West Hampton Dunes, New York, 2001–2003.

Prey type	Cover type	Date	*n*	No. >0[a]	Organism counts		
					Min	Max	Median
Terrestrial	Bay ITZ[b]	19 Mar 2001	5	0 (0%)	0	0	0
		24 Mar 2002	5	2 (40%)	0	5	0
		25 Mar 2003	5	0 (0%)	0	0	0
	Ocean ITZ	19 Mar 2001	6	0 (0%)	0	0	0
		24 Mar 2002	6	1 (17%)	0	1	0
		25 Mar 2003	6	0 (0%)	0	0	0
	Upland[c]	19 Mar 2001	40	1 (3%)	0	1	0
		24 Mar 2002	43	20 (47%)	0	8	0
		25 Mar 2003	48	4 (8%)	0	2	0
Benthic	Bay ITZ	18 Mar 2001	6	6 (100%)	3	18	11
		24 Mar 2002	6	6 (100%)	4	135	43
		25 Mar 2003	9	9 (100%)	11	349	34

[a] No. >0 = number of samples (sticky traps or sediment cores) with at least one prey organism.
[b] ITZ = intertidal zone.
[c] Upland = pooled samples from all strata (cover types) at or above the tide line. These include fresh wrack, old wrack, backshore (bare and vegetated strata), and dune.

would not be expected to host benthos. Terrestrial arthropods were virtually absent from all zones, even though large numbers are caught in sticky traps later in spring and summer (Cohen et al. 2009). Thus, early season prey abundance and distribution could affect Piping Plover territory location and size, and could help explain why nesting pair density of Piping Plovers is high where sand flats are available (Patterson et al. 1991, Elias et al. 2000, Cohen et al. 2009). There often is a tidal lag between the bay and ocean side of barrier islands as water passes through tidal inlets, and the presence of bay side intertidal flats could increase the potential time each day that benthic organisms are available as prey.

A connection between early season foraging opportunities and fitness may not require adults to forecast prey availability for chicks. Reproductive success in many avian studies decreases with time from onset of breeding (Martin 1987). Insect abundance during egg-laying and chick-rearing were uncorrelated for Tree Swallows (*Tachycineta bicolor*), but reproductive success was correlated with insect abundance during egg-laying by affecting timing of breeding and egg mass (Nooker et al. 2005). Thus, it likely benefits female Piping Plovers to nest adjacent to high-quality foraging habitat that allows them to quickly enter breeding condition. Maternal nutrition has been shown to influence quality of offspring of many avian species with offspring ranging from fully altricial to fully precocial (Blomqvist et al. 1997, Parker 2002, Reynolds et al. 2003, Verboven et al. 2003).

Perhaps more importantly in our study area, intertidal flats usually host a higher abundance of arthropods in late spring than other cover types (Loegering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009). Thus, the same cover type provides prey for adults upon arrival and different but still abundant prey for chicks later in the season. However, chicks in some breeding areas cannot access intertidal sand flats, and there is a difference between pre-laying and chick-rearing foraging areas. Piping Plover broods in Virginia without access to bay side flats starved, because the ocean beaches were arthropod-poor and only chicks that accessed intertidal flats survived (Loegering and Fraser 1995). Some adults in that case settled within easy flight range of early-season foraging habitat but, when their eggs hatched, there was insufficient food for their chicks. Sand flats were used by foraging adults in a site adjacent to our study area in New York, but were not available to any broods (Cohen et al. 2009). Chick survival was unaffected in that case (Cohen et al. 2009).

Most strategies commonly used for Piping Plover conservation focus on enhancing survival of eggs and chicks to improve productivity (fledglings produced per breeding pair), and protections often are established after birds have settled on their territories (USDI 1996). However, true productivity is number of recruits into the breeding population per breeding pair (Martin 1987). The correlation between recruitment and fledglings produced depends in part on natal site philopatry which can be a function of density and habitat quality (Sedgwick 2004, Wrege et al. 2006), and which was low (~ 12%) at our site (Cohen et al. 2006). Site fidelity of adults and immigration of new breeders may depend on habitat conditions during pre-laying (Wrege et al. 2006). Thus, protecting habitat from disturbance or degradation during the pre-laying period is important.

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Interspecific Song Imitation by a Cerulean Warbler

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ABSTRACT.—We report a male Cerulean Warbler (*Dendroica cerulea*) singing a highly accurate version of another species' song (Hooded Warbler; *Wilsonia citrina*), as well as a typical Cerulean Warbler song. We performed playback experiments to examine the manner in which this bird used, and responded to, the different songs. He responded aggressively (wing flicks and garbled song), and with his Cerulean Warbler song, to recorded versions of two different types of Cerulean Warbler songs, including a type that he was not observed singing. He did not respond in any manner to playback of Hooded Warbler song. *Received 5 October 2009. Accepted 2 February 2010.*

Few cases of high-quality interspecific imitation exist in the wild, outside of natural voice mimics. Differences in acquired or innate auditory templates are thought to limit interspecific song learning (Marler 1976, 1984). Interspecific imitation, when it does occur, typically is between closely-related species or species that compete for space and resources (Kroodsma 2004). Members of the Parulidae, of non-mimicking species, are among those best known to learn and copy songs of other species (Payne et al. 1984, Spector 1992, Martin et al. 1995).

Males in many genera of Parulidae (including *Dendroica*) sing two distinct song types that may serve different functions (Kroodsma 1981, Spector 1992). Type I songs, in the case of Cerulean Warblers (*Dendroica cerulea*), are primarily used in an intersexual context (e.g., mate attraction) and are sung more often early in the breeding season when the male is unmated (Woodward 1997). Type II songs are those that typically have an intrasexual function (e.g., territorial defense) and are sung more often later in the breeding season, after a mate is secured (Woodward 1997). We describe a case of a male Cerulean Warbler singing an indistinguishable version of another species' song (Hooded Warbler; *Wilsonia citrina*), as well as a typical Cerulean Warbler song. We also describe the results of playback experiments performed with this individual.

OBSERVATIONS

On 25–27 June 2009, we observed an after-second-year, unpaired male Cerulean Warbler in the North Cumberland Wildlife Management Area (36° 12′ 41.1″ N, 84° 16′ 55.1″ W), in the Cumberland Mountains of Tennessee, USA, singing both a Cerulean Warbler song and an accurate copy of a Hooded Warbler song. We delineated this individual's territory and ascertained his pairing status based on extensive spot-mapping, nest searches, and banding efforts. Two other paired male Cerulean Warblers maintained territories adjacent to this individual but, to the best of our knowledge, this individual was unpaired and did not breed during the 2009 season. We did not observe him singing a Hooded Warbler song until 25 June, although he had been defending this territory since early May. The high density of Hooded Warblers, and the quality of this individual's imitation, served to mask this behavior from our observations until this occasion.

We first observed this individual on 25 June 2009 at 1500 hrs singing a Cerulean Warbler song at a rate of six/min over a 5-min period (Fig. 1). At 1505 hrs, he began singing a Hooded Warbler song at a rate of eight/min over a 15-min period (Fig. 2). At 1525 hrs, he began to sing the Cerulean Warbler song again for a 10-min period. He continued to alternate between songs for the next 15 min. We then attempted to capture the bird using playback of a similarly structured Cerulean Warbler song, a Cerulean Warbler decoy placed at 2 m, and a mist-net. We placed the speakers at ground level and adjusted the volume of the speakers to the approximate intensity level produced by the bird. The bird immediately responded with a typical Cerulean Warbler vocal response to conspecific playback (a garbled, softly sung, Cerulean Warbler song). He also performed the same Cerulean Warbler song that he was observed singing earlier.

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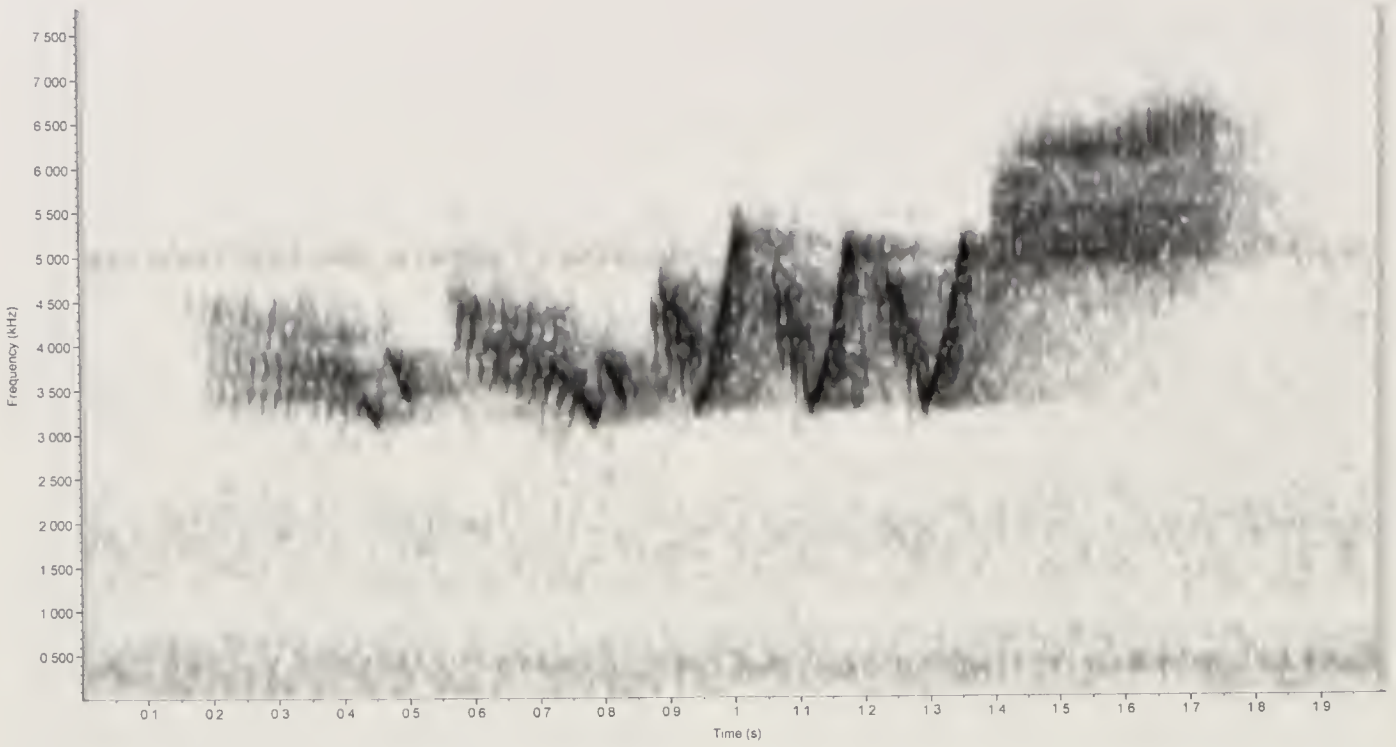

FIG. 1. Spectrogram of Cerulean Warbler song, performed by the bird in question. This song was indistinguishable by ear from songs performed by other male Cerulean Warblers. A previously recorded version of this song type was played to the male Cerulean Warbler in question on 25 June 2009 and he responded aggressively.

Physically, he responded typically as well, with nervous wing flicks and foraging imitations as he approached within 5 m of the speakers and decoy. The bird was caught shortly thereafter, banded, photographed, and released. He appeared to be a phenotypically normal, after-second-year male Cerulean Warbler (based on Pyle 2000), displaying traits that may be indicative of age and good condition (e.g., a strong breast band and large amount of white spotting on his tail; TJB, unpubl. data). The bird returned to singing a Hooded Warbler song 4 min after release.

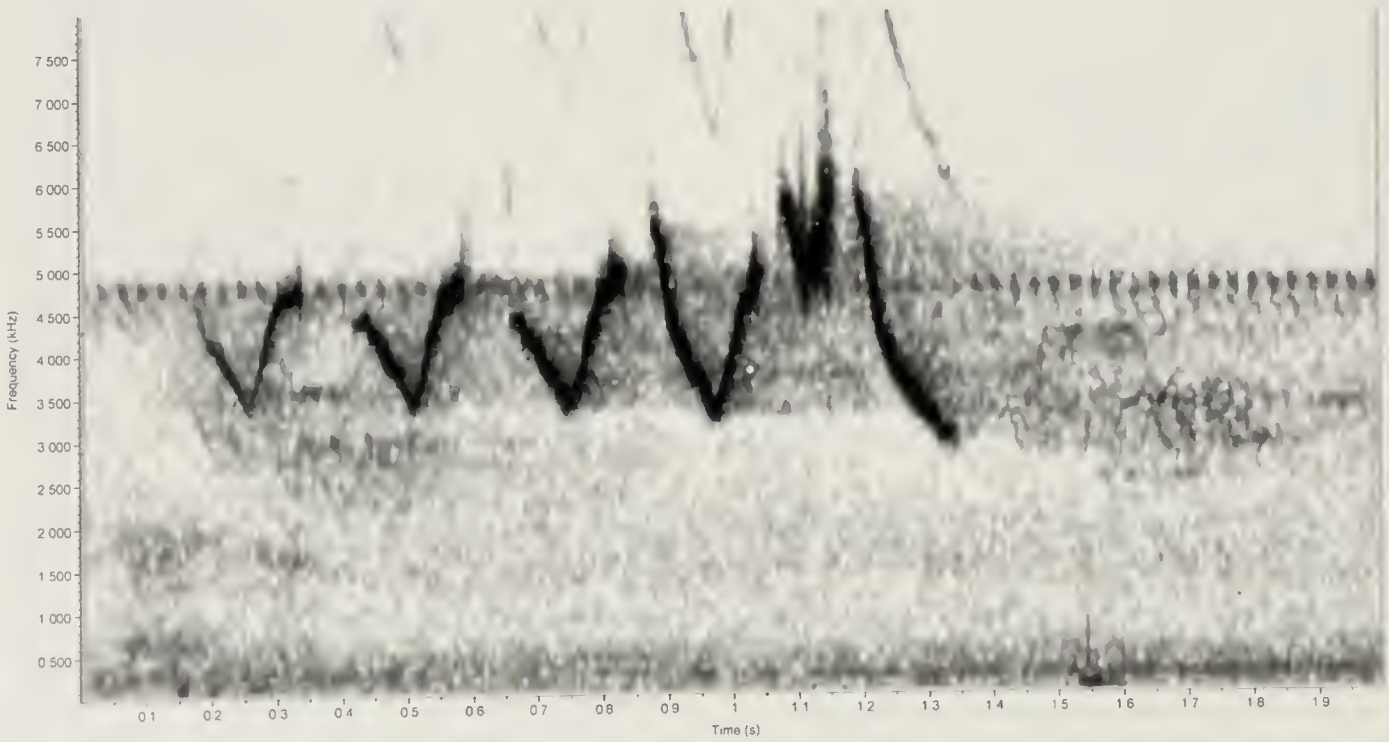

FIG. 2. Spectrogram of Hooded Warbler song performed by the Cerulean Warbler in question. This song was indistinguishable by ear from actual Hooded Warbler songs.

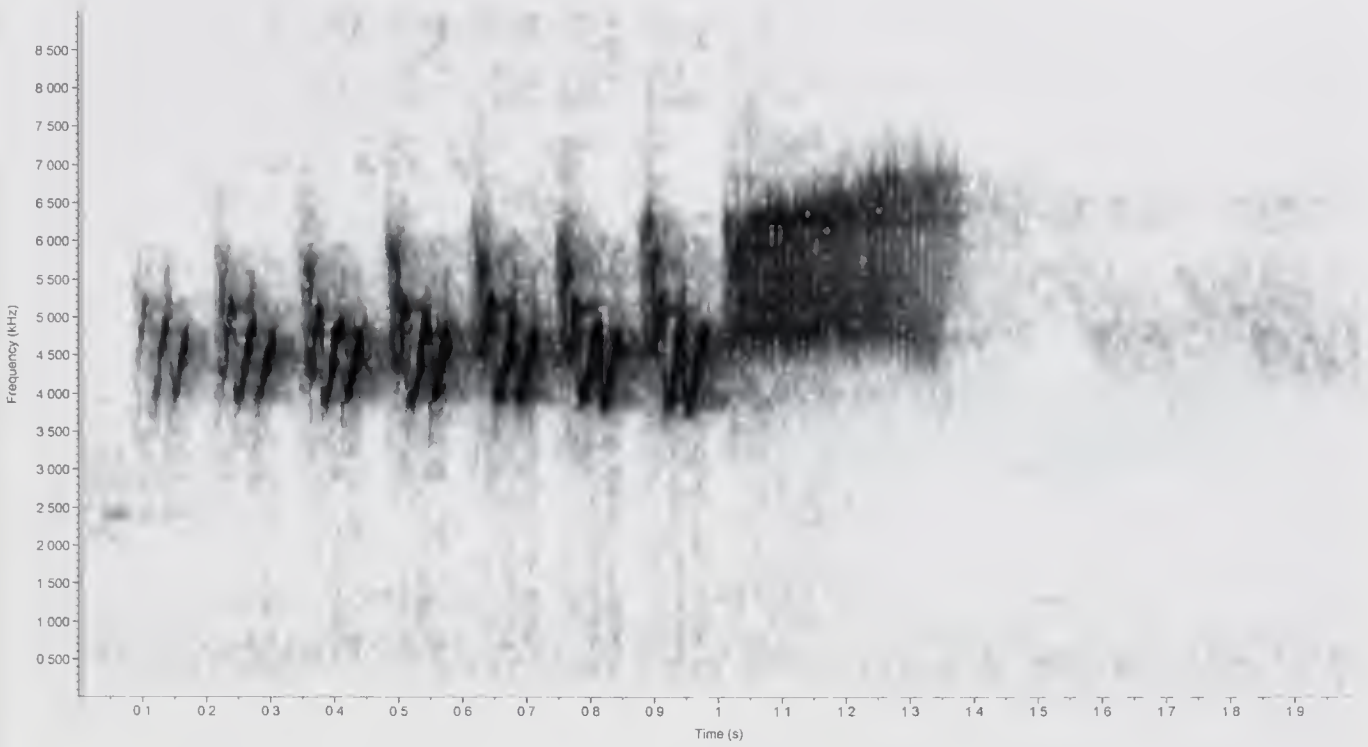

FIG. 3. Spectrogram of alternative Cerulean Warbler song type used in playback experiment with the bird in question on 26 June 2009. He responded to this song type in the same aggressive manner as he responded to the Cerulean Warbler song type that he was heard singing.

We returned to the location on 26 June and made sound recordings of both songs using a Dan Gibson Parabolic Microphone and a M-Audio Microtrack II digital recorder. We detected the bird at 0800 hrs, without use of playback, singing the same type of a Cerulean Warbler song. He sang this song for 15 min at a rate of six/min. After that, he sang his Hooded Warbler song for 9 min, at a rate of nine/min. Following our recording of the bird's repertoire, we broadcast a recorded version of a similar Hooded Warbler song for 10 min and he did not respond, vocally or physically. We then broadcast an alternate version of a Cerulean Warbler song with no decoy (Fig. 3). The bird again responded within 2 min, approaching the speakers and displaying similar aggressive behavior (wing flicks, garbled song). He then retreated into the canopy and sang his Cerulean Warbler song (Fig. 1). We returned on 27 June to see if he would respond to Hooded Warbler playback and, once again, he did not. We did, however, observe him again singing the same type of Cerulean and Hooded warbler songs.

We recorded individual male Cerulean Warblers earlier in the season for unrelated research and, after these observations, we recorded neighboring Hooded Warblers for comparison (Figs. 4, 5). We created spectrograms of all songs using Raven Pro acoustic analysis software (Cornell Laboratory of Ornithology, Ithaca, NY, USA).

DISCUSSION

This individual likely learned his song repertoire from both Cerulean and Hooded warbler tutors. This would be possible at many locations in the Appalachian Mountains, as both Hooded and Cerulean warblers are relatively common in similar habitats. These two species, however, use different strata of the forest canopy (Cerulean Warblers use the overstory and Hooded Warblers use the understory), belong to separate, well-resolved genera (Lovette and Birmingham 2002), and have distinctly different songs. Our observations differ from the pattern of interspecific learning suggested by Kroodsma (2004); imitators usually belong to closely related species or compete for space and resources. There are several species of wood-warblers within the same genus and occupying similar forest strata, which seem more likely to act as interspecific tutors for Cerulean Warblers (e.g., Black-throated Green [*Dendroica virens*] or Blackburnian warblers [*D. fusca*]).

Our playback experiment results suggest this individual used, and responded to, Cerulean Warbler song in an intrasexual (Type II) manner. His response to Cerulean Warbler playback (wing flicks, garbled songs) was typical of territorial behavior by Cerulean Warblers and, during playback bouts, he only performed his Cerulean

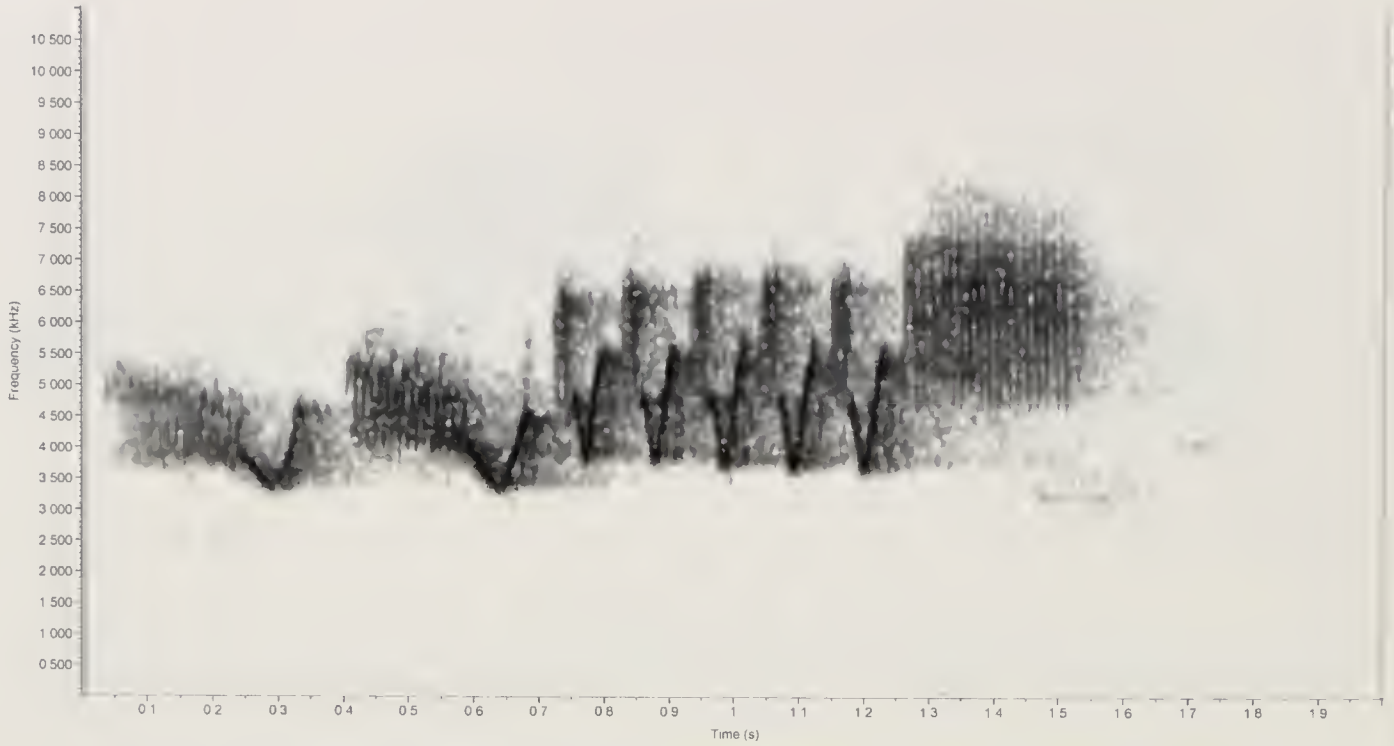

FIG. 4. Spectrogram of Cerulean Warbler song performed by a neighboring Cerulean Warbler.

Warbler song. This male was unpaired and singing at a late date (highly unusual for after-second-year birds in this region), suggesting that his unusual song repertoire was the cause of his lack of reproductive success. We were unable to ascertain how he used his Hooded Warbler song or how he perceived other Hooded Warbler songs. He did not respond (physically or vocally) to Hooded Warbler song, suggesting that he did not use or perceive Hooded Warbler song in a Type II manner.

This individual may be at a disadvantage when defending a high-quality territory because his use

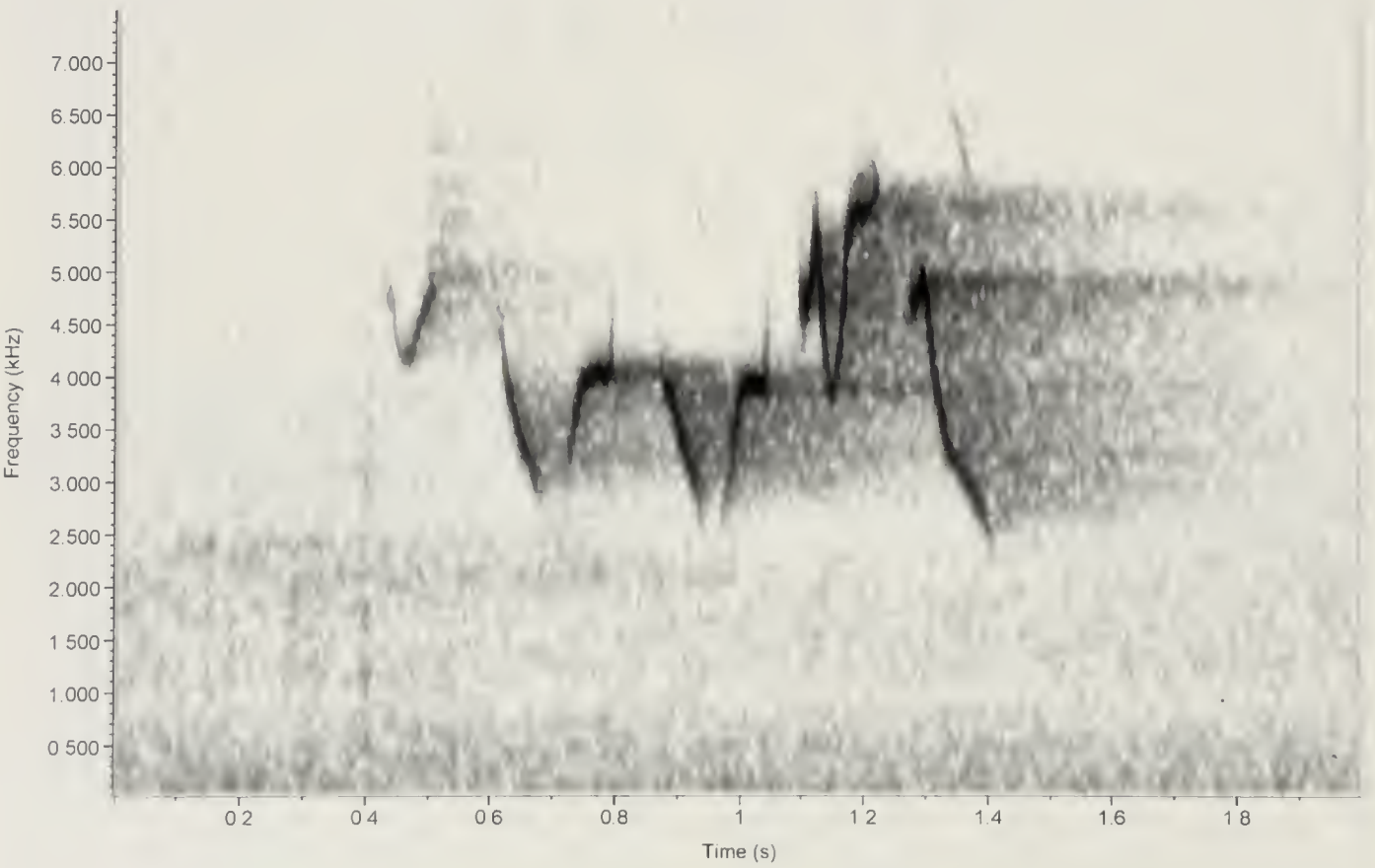

FIG. 5. Spectrogram of Hooded Warbler song performed by a neighboring Hooded Warbler.

of an interspecific song may increase the chance of conspecific fights, therefore increasing the costs of defense (Martin et al. 1995). This was the case during the 2009 season; the territory he occupied was adjacent to only two conspecific territories, which is low for appropriate habitat in the densely-populated Cumberland Mountains. His territory also had lower than average DBH and canopy height, similar to areas often unoccupied by (or occupied by younger male) Cerulean Warblers in the area (TJB, unpubl. data).

In the event this individual returns in 2010, we will attempt to observe his interactions with neighboring Hooded Warblers, record changes in song preference throughout the breeding season, and observe changes in responsiveness to playback of different songs at different times during the season.

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Nests, Nest Placement, and Eggs of Three Philippine Endemic Birds

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ABSTRACT.—We describe the nest and eggs of two Philippine endemic passerines, the Rusty-faced Babbler (*Robsonius rabori*) and the Blue-breasted Blue Flycatcher (*Cyornis herioti*). We also describe a novel type of nest and nest placement for the Short-crested Monarch (*Hypothymis helenae*), and provide the first description of the eggs of this species. We discuss similarities among eggs and nests of these species with their relatives, and the need for more information regarding natural history and breeding habits for the Philippine avifauna. *Received 13 October 2009. Accepted 10 February 2010.*

Ornithologists have long been aware of the distinctiveness of the Philippine avifauna, which is reflected in the high percentage of endemism in the archipelago (Dickinson et al. 1991). However,

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FIG. 1. Left. Nest of *Robsonius rabori*. Arrow shows the entrance location (Photograph by Nevong Puna). Right. Egg of *Robsonius rabori* (Photograph by Luis A. Sánchez-González). Site: ~12 km WSW of Baler, Municipality of San Luis in Aurora Province (15° 39.22′ N, 121° 30.44′ E), June 2009.

the Philippine avifauna is one of the most poorly known in the world (Kennedy et al. 2000). Breeding habits for some endemic species are well known, and the first descriptions of the breeding habits or nestlings of other species are starting to appear in the literature (Strijk 2004). However, breeding habits for a large portion of the Philippine avifauna remain undocumented. Dickinson et al. (1991) estimated that ~395 species may breed in the country and 157 of these apparently lack any breeding information. Not surprisingly, 77 of these poorly known species are endemic, which represents about one half of the Philippine endemics.

Knowledge of species natural history and nesting biology is fundamental for development of sound protection strategies. This information is also useful for taxonomic purposes. For example, studies on nest architecture can provide a new set of taxonomic characters used for phylogenetic analysis (Zyskowsky and Prum 1999), while data on clutch size, egg color, and egg patterns can be used to infer evolutionary relationships (e.g., Mayr 1931, Ford 1981, Zelenitsky and Modesto 2003). We report the first description of the nest, nest placement, and eggs for two species of Philippine endemic birds, *Cyornis herioti* and *Robsonius rabori*, and provide the first description of the eggs of *Hypothymis helenae* as well as a completely new type of nest placement for this species.

METHODS

Study Area.—All data for this paper were collected during a survey conducted from mid May to late June 2009 in the Sierra Madre Mountains of Aurora Province, in the northeastern part of Luzon Island. The main vegetation type in the area is dipterocarp forests, although montane forests are found above 1,200 m. The three sites were at elevations ranging from 50 m at Baler to 530 m at the two other sites visited. The average

FIG. 2. Left. Location of the nest cavity of *Cyornis herioti*. The white arrow shows the cavity in the rock (Photograph by Luis A. Sánchez-González). Right. Nest and eggs of *Cyornis herioti*; Aurora National Park, Aurora Province (15° 67.80 N, 121° 33.61 E), May 2009. Photograph by Robert G. Moyle).

rainfall is 300 mm per year and is evenly distributed throughout the year (Dickinson et al. 1991).

Field Procedures.—Data were gathered during observation walks spanning the hours of avian activity. Observations were made with binoculars (7 × 35, 10 × 50) and we used a specialized field guide (Kennedy et al. 2000) for bird identifications.

NEST DESCRIPTIONS

Robsonius rabori.—The Rusty-faced Babbler (Timaliidae) is an uncommon and local species known only from the northern half of Luzon Island (Collar and Robson 2007), where it occurs in rocky or part-rocky areas in lowland forest and second growth up to 1,000 m (Kennedy et al. 2000). Almost nothing is known about the breeding habits of this elusive species, and its breeding dates have only been extrapolated from observations of fledglings in February and March, and in May and August (Kennedy et al. 2000).

We found a nest of this species on 18 June 2009 along an overgrown dirt logging road in second growth forest at 525 m, ~12 km WSW of Baler, Municipality of San Luis in Aurora Province (15° 39.22′ N, 121° 30.44′ E). The nest consisted of a large clump of dry sticks, branches, and leaves with a front entrance (8 cm in diameter). The dome was 19 cm wide and propped up by twigs 50 cm from the ground against a bank of rock and mud (Fig. 1 Left). The nest was <1 m from a 0.5 m high rock slide. A small stream was ~30 m from the nest down a steep slope. The nest contained a single elongated egg (28.9 × 18.55 mm) with a whitish-cream base color and gray and light-brown blotches (Fig. 1 Right). The female occupant of the nest was collected (catalog number KUNHM 114678); another egg about to be laid was in its oviduct indicating a clutch size of two eggs. Both are now in the Natural History Museum of the University of Kansas (KUNHM).

The nest architecture of this species is similar to that reported for a *R. sorsogonensis* (Collar and Robson 2007); they build large balls of clumped dried twigs and leaves. This architecture differs from babblers in the genera *Trichastoma*, *Kenopia*, and *Turdinus*, which currently stand close to *Robsonius* in linear classifications, but is similar to that of *Gypsophila* and *Napothera*, which also build dome nests (Collar and Robson 2007). However, the eggs of *R. rabori* superficially

FIG. 3. Nest and eggs of *Hypothymis helenae* inside a tree-fern stump. Baler, Aurora Province (14° 44′ N, 121° 33′ E), June 2009. Photograph by Luis A. Sánchez-González.

resemble those of the genus *Turdinus*, as illustrated in the case of *T. macrodactylus* from Java (Hoogerwerf 1949).

Cyornis herioti.—The Blue-breasted Blue Flycatcher (Muscicapidae) is endemic to Luzon and Catanduanes islands where it inhabits primary and selectively-logged forests between 100 and 1,200 m (Taylor 2006). This sexually dimorphic species occurs in mixed species flocks, solitary or in pairs, and its breeding habitats are mostly unknown. The breeding season, which may occur in May, has been inferred from observations of individuals with enlarged gonads, nestlings, and recently fledged juveniles. However, both the nest and eggs are unknown (Kennedy et al. 2000, Taylor 2006).

A nest and eggs of this flycatcher were found on 23 May 2009 in Aurora National Park, Aurora Province (15° 67.80 N, 121° 33.61 E). The nest was in a shallow cavity in a 4-m tall rock along the course of a river (Fig. 2 Left). The nest was cup-shaped and had thick walls (inside dimensions 60 × 50 mm; outer dimensions 100 × 120 mm). The inside was lined with fern fronds and the outside was covered with moss. Depth of the nest cup was 35 mm, whereas the total depth of the nest was ~55 mm. The nest contained two broken eggs and one whole egg (21 × 16 mm), which were light brown with slightly darker specks (Fig. 2 Right). The female was observed incubating the eggs during the night. All attributes of the nest including placement in a shallow cavity and clutch size seem to be typical of nesting habits in the genus, as well as in other genera of Muscicapidae, such as *Cyanoptila* and *Eumyias* (Taylor 2006).

Hypothymis helenae.—The Short-crested Monarch is an endemic species of the Monarchidae that inhabits humid forests up to 1,000 m, where it usually occurs singly or in pairs in mixed species flocks. Breeding has been reported to occur around August, although some individuals taken in April and May also seemed to be in breeding condition as inferred from enlargement of the gonads (Kennedy et al. 2000, Coates et al. 2006).

Allen et al. (2006) described the nest of this species from Camiguin Norte Island but eggs were not observed.

We found a nest of this species on 8 June 2009 in secondary growth forest at Baler, Aurora Province (14° 44′ N, 121° 33′ E). The nest was inside the broken trunk of a tree fern ~70 cm from the ground. The cavity was 55 mm deep and 65 mm in diameter. Nest material included dry leaves and small branches of tree fern (Fig. 3), all roughly shaped into a cup. The nest contained two eggs, one of which was laid the day after discovery of the nest. The eggs (21 × 16 mm) were bluish green with brown and dark brown blotches; the distal part of the egg was heavily blotched. The female, which has a different plumage from the male, was flushed from the nest at dusk of the second day.

Nest architecture and placement of this species differs somewhat from its conspecific *H. helenae personata* from Camiguin Norte and its close relative *H. azurea*, for which nests are typically cup-shaped structures decorated outside with lichen and moss, usually in the fork of a tree branch (Hoogerwerf 1949, Allen et al. 2006, Coates et al. 2006), whereas the heretofore undescribed nest of *H. helenae helenae* from Luzon was placed in a hollow trunk. Nest architecture and nest placement within the genus *Hypothymis*, and specifically within *H. helenae*, needs further study. Natural history and phylogenetic studies of the genus are also needed to examine the significance of these differences.

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Nests, Eggs, and Young of the Azure-crowned Hummingbird (*Amazilia cyanocephala*)

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ABSTRACT.—The first of several nests (previously undescribed) of the Azure-crowned Hummingbird (*Amazilia cyanocephala*) was found on 20 February 2009 along the Río Pixquiac in Coatepec, Veracruz on the Gulf of Mexico side of the Sierra Madre Oriental of Mexico. The cup-shaped nest consisted of fibers and scales of tree ferns with the outside covered with liverworts and a few mosses and lichens. It was saddled on a thin, horizontal branch and had one "tail" of hanging liverworts, longer than the height of the nest cup, draped beneath the nest. It eventually contained two white, non-glossy eggs that were long-elliptical in shape, measuring roughly 13.5 × 7.5 mm. Other nests of the species discovered subsequently were similar in construction and placed on branches or substrates of different plant species. Observations of nest building, eggs, and incubation behavior at the first nest were generally consistent with descriptions for other *Amazilia* hummingbirds. *Received 29 September 2009. Accepted 21 January 2010.*

Little is known about the nests, eggs, incubation, fledglings, and breeding behavior of members of the genus *Amazilia* (Skutch 1931, Harverschmidt 1952, Atwood et al. 1991), which comprises ~30 species in Central and South America (AOU 1998, Remsen et al. 2008). Published records of nests and eggs are available for less than half of the species (del Hoyo et al. 1999). Thus, knowledge of nesting of *Amazilia* is far from complete (Ornelas 1995, Weller 1998).

The Azure-crowned Hummingbird (*Amazilia cyanocephala*) is a common resident in Mexico from Tamaulipas south through the Isthmus of Tehuantepec to Chiapas, and through Central America to Honduras and northern Nicaragua (Howell and Webb 1995, Johnsgard 1997). This medium-sized hummingbird is characterized by the immaculate white throat and belly with golden green flanks and indicated breast band, uniformly green to bronzy upperparts and olive-green centers of under tail coverts, and a bright, glittering blue forehead and crown (more turquoise in female-type plumage). It is similar in size and general appearance to the Violet-crowned Hummingbird (*A. violiceps*), but *A. cyanocephala* has a blackish upper mandible and a reddish lower mandible with dark tip, whereas the bill of *A. violiceps* is fleshy red except for the dark tip (Weller 1998). Both taxa are apparently entirely allopatric (Johnsgard 1997); locally sympatric, the White-bellied Emerald (*A. candida*) is much smaller and easily distinguished in the field by the dark subterminal band of its tail.

The species is fairly common in oak (*Quercus* spp.) and pine (*Pinus* spp.) woodlands, cloud forests, humid evergreen forest edges, pine savannas, gardens, and brushy and second growth habitats from 500 to about 2,400 m elevation (Davis 1972, Peterson and Chalif 1973, Howell and Webb 1995, Johnsgard 1997). Birds on the Atlantic Slope from southern Tamaulipas to Veracruz in Mexico, and in the interior from eastern Oaxaca and Chiapas to western Nicaragua are assigned to the *cyanocephala* subspecies. Resident birds of the Mosquitia coastal region in Honduras are assigned to the *chlorostephana* subspecies with crown glittering green to turquoise-green (Howell and Webb 1995). Range of the *chlorostephana* subspecies below 100 m is tied to the distribution of pine (*P. caribae*) savanna, stands of pine close to gallery forest, and edges of isolated evergreen rainforest (del Hoyo et al. 1999). Birds from Belize south to northern Nicaragua, formerly separated as *guatemalensis*, show strong intergradation with nominate birds from Chiapas, Mexico (Howell and Webb 1995).

Little information on nesting behavior of the Azure-crowned Hummingbird is available, but two species of the widespread genus *Amazilia* have been studied (Skutch 1931, Harverschmidt 1952), and major differences from these are unlikely (Johnsgard 1997). Azure-crowned Hummingbirds with enlarged gonads have been

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FIG. 1. Nest placement, nests, eggs, and nestlings of Azure-crowned Hummingbird (*Amazilia cyanocephala*) photographed along the Río Pixquiac near Xalapa, Veracruz. (A) Completed nest first under construction on 20 February 2009 (nest #1, Table 1). (B) Two eggs laid in an interval of 2 days, 25 and 27 February (alternate laying). (C) Eggs hatched almost synchronously after 15 days of incubation, the first egg hatched by noon on 15 March. (D) Eight-day old nestlings. (E) Incomplete nest (nest #2) built after failure of nest #1. (F) Nest #2 was not completed but the first egg was laid on 5 April. (G) and (H) present two views of nest #5. Photographs by the author.

TABLE 1. Measurements (mm) of *Amazilia cyanocephala* nests and eggs (min and max exterior and interior diameter of cup-shaped nests).

	Nest measurements				Egg measurements		
Nest #	Total depth	External diameter	Inside diameter of cup	Depth of cup	Egg 1	Egg 2	Reference
1	45	45 × 45	28 × 32	20	13 × 7	14 × 8	This study
2	30	44 × 45	27 × 28	17			This study
3	50	42 × 55	25 × 32	22			This study
4	40	51 × 57	30 × 34	22			This study
5	51	43 × 55	24 × 32	21			This study
6	45	44 × 51	25 × 32	20			This study
7	45	38 × 45	25 × 30	22			This study
8	50	45	27	22	14.2 × 9.0	14.2 × 9.2	Rowley (1984)

reported from February to August (del Hoyo et al. 1999) and two nests were found in April in Oaxaca, Mexico (Rowley 1984). Nests of *A. cyanocephala* have been found before, but none has been described and observed in detail; detailed nesting information is unavailable for most species in this genus (del Hoyo et al. 1999). The objective of this paper is to describe the nest, eggs, and incubation of the Azure-crowned Hummingbird (*A. c. cyanocephala*) in Veracruz, Mexico.

OBSERVATIONS

The study area consisted of cloud forest and secondary riparian growth bordering the Río Pixquiac (19° 30′ 25″ N, 96° 57′ 39″ W; 1,348 m above sea level) 6 km west of the city of Xalapa, Veracruz, Mexico. Río Pixquiac is a small tributary of Río Consolapa, which traverses Coatepec on the eastern foothills of the Cofre de Perote volcano on the Atlantic side of the Sierra Madre Oriental. I observed a hummingbird at 0715 hrs on 20 February 2009 fly directly into a *Phyllostachys* bamboo bush at a distance of about 15 m. I trained binoculars at where the bird appeared to land and observed it sitting on a nest 1.5 m above the ground adding nesting material. I watched the hummingbird for ~15–20 min, during which time it visited the nest twice. I was able to confirm the bird was building the nest at 0730 hrs the following morning. I watched the female building the nest for ~30 min, during which time she made two visits. I returned later in the morning (at 1015 hrs) to obtain photographs of the nest. The female was not seen during this 15-min visit. I checked the nest daily at ~0800 hrs.

The female made one trip to the nest every 30 min during the course of the early morning observation on 20 February, when the nest was first found, typically remaining for a minute or more. Her building rate early on the following morning was similar and the nest was nearing completion (Fig. 1A). However, the female when watched from much closer range, showed signs of nervousness and flew from the nest at each visit. I stopped close-range observations on nest building to avoid cessation of activity and to reduce risk of nest abandonment.

The female, at times, spent a short time during nest-building visits sitting motionless in the nest cup in an incubation posture on 25 February. I checked the nest in her absence by noon, and the nest contained one egg. The female arrived a few minutes later, perching 5 m from the nest and carrying material for the nest (lichens). I moved away from the nest after taking photographs and egg measurements, and the female entered the nest and placed nesting material on the outer wall. No signs of incubation occurred that day or the following day. A second egg (Fig. 1B) was found (egg measurements in Table 1) on 27 February. Eggs were laid in the early morning and there was an interval of 2 days before the second egg was laid. Incubation began after the second egg was laid, after which the nest and eggs were checked twice daily, early in the morning and in the afternoon until the eggs hatched. Building (~8–10 days) and maintenance of the nest, which consisted primarily of attaching lichens to the outside of the nest (there were few lichens at the start of observation), continued throughout the incubation period.

The incubation period lasted 15 days and eggs hatched almost synchronously. The first egg

FIG. 2. Illustration of the construction of *Amazilia cyanocephala* nests collected along the Río Pixquiac near Xalapa, Veracruz. Open cup-shaped nest at the two ends of the supporting, horizontal *Phyllostachys* bamboo branch kept the top of the nest cup level with respect to the ground (below). Nest cup on the top of an old *Heliconia* infructescence (above). Drawing by Edmundo Saavedra.

hatched (Fig. 1C) by noon on 15 March and the second hatched ~1800 hrs that day. Eggshell remains were removed from the nest the following day. The female brooded the young after feeding and during the night on subsequent days. Nestlings were photographed when they were 8 days of age (Fig. 1D). I checked the nest early in the morning on 23 March, when the nestlings were 9 days of age, and found it empty. The nest was intact with no signs of disturbance or stealing of nesting material by other hummingbirds (Skutch 1931). I believe Social Flycatchers (*Myiozetetes similis*) attacked the nestlings, as I observed several perched near by and had witnessed their attacks on nestlings of Northern Rough-winged Swallow (*Stelgidopteryx serripennis*) in the same area. The nest was collected 2 days later to make a full description and illustration (Fig. 2). The female remained in the area for several days.

The cup-shaped nest was built in a 2 m tall *Phyllostachys* bamboo, isolated by young second growth and *Heliconia* plants near the Río Pixquiac. It was saddled on a lower, slightly downward sloping branch 1.5 m above the ground. The horizontal supporting branch was imbedded within the nest wall and provided additional support on the lower side of the nest. One "tail" of nest material hung beneath the supporting branch (Fig. 2, nest measurements in Table 1). The nest cup was constructed in two layers like most hummingbird nests. The outer layer was comprised of strips of grasses, small dried pieces of leaves and flowers of *Mimosa* spp., scales from tree ferns (*Alsophila firma*, *Cyathea bicrenata* and *Cyathea* aff. *fulva*) (Cyatheaceae), whereas the somewhat thicker inner layer was comprised of *Tillandsia deppeana* seed down (Bromeliaceae) and many hairs from horses. The outside of the nest was heavily decorated with many pieces of greenish-white lichen, liverworts *Calypogeja* spp. (Calypogejaceae), and less so with mosses; all were adhered with spider web.

I discovered the female building a second nest (nest #2; Table 1) on 2 April, only 30 m to the west of nest #1, fastened on the outmost, unsheltered branch of a *Bougainvillea* shrub, 1.7 m above the ground. The nest was half completed and had no lichens on the outer wall (Fig. 1E). I continued my observations of this nest by daily checking it at ~0800 hrs. The female continued steadily at her growing nest during consecutive days. The first egg was laid on 5 April, but the nest was not completed (Fig. 1F). A period of inclement weather was initiated the following day that presumably caused the female to interrupt building and nest attendance, resulting in failure to lay a second egg on 7 April. The single egg lay cold in the nest for an additional 3 days and on 10 April it was destroyed, leaving only eggshell fragments. The nest was collected 2 days later for measurements. The female was observed in the area for several days, but a third nest attempt was not observed.

I am confident the female, which built the second nest, was the same individual whose nestlings were depredated. A female (apparently the same) nested in this area for 3 consecutive years; nest #3 was placed on a dried *Heliconia* infructescence (Fig. 2) and nest #4 was placed on a *Bougainvillea* shrub. I searched the Río Pixquiac area on 10 April and located three more *A. cyanocephala* nests similar to those described. Nests were placed on a branch of a palm (*Acrocomia* spp.) tree (Fig. 1G–H), a *Heliconia* infructescence, and on a branch of a *Quercus* tree, all no more than 3 m above the ground. The three nests were each active with two nestlings. Nests were collected and measured (Table 1) after young fledged.

This study provides the first descriptions and measurements of the nests of *Amazilia cyanocephala*. Evidence is presented that supports the belief that predation and weather may be the main causes of nesting failure of tropical hummingbirds (Skutch 1931, Fierro-Calderón and Martin 2007), as well as temperate hummingbirds (e.g., Baltosser 1986, 1996).

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Nest Description of the Garden Emerald (*Chlorostilbon assimilis*) from Costa Rica

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ABSTRACT.—The Garden Emerald (*Chlorostilbon assimilis*) is endemic to southwestern Costa Rica and Panama, and knowledge about its' reproductive habits is limited. We describe the nest and nestlings of the Garden Emerald based on a nest found in La Amistad International Park. The nest was built on an anthropogenic substrate, and was similar to nests described for other emerald species. However, unlike other emeralds, the nest contained no lichens, mosses, or ferns. The nestlings resembled adult female plumage, similar to that for other nestling emerald species. *Received 24 August 2009. Accepted 3 February 2010.*

The neotropical genus *Chlorostilbon* includes 17 species of small hummingbirds (AOU 1998, Remsen et al. 2009), 11 of which have described nests (Wolf 1964, Hilty and Brown 1986, Stiles and Skutch 1989, Thomas 1994, Howell and Webb 1995, Stiles 1996, Oniki and Antunes 1998, Schuchmann 1999, Garrido and Kirkconnell 2000). The Garden Emerald (*Chlorostilbon assimilis*) is endemic to southwestern Costa Rica and Panamá to western Darién, including pacific islands, and rarely from Bocas del Toro along the Caribbean coast of Panamá (Ridgely and Gwynne 1989, Stiles and Skutch 1989). This hummingbird inhabits secondary forest and open areas with isolated shrubs at elevations up to 1,500 m (AOU 1998, Garrigues and Dean 2007). The nest of the Garden Emerald is undescribed (Stiles and Skutch 1989, Schuchmann 1999) and we provide the first nest description for this species. We also include a brief description of the nestlings.

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FIG. 1. Nest of Garden Emerald found on 28 March 2009 near the Altamira Ranger Station, La Amistad International Park, Costa Rica. (Collected on 18 April 2009; photograph by Luis Sandoval).

OBSERVATIONS

We found a nest of Garden Emerald on 28 March 2009 at the Altamira Ranger Station in La Amistad International Park, Buenos Aires, Puntarenas, Costa Rica (09° 02.9′ N, 83° 00.8′ W; 1,375 m asl). The site is an open area with a park ranger station, surrounded by a garden, which included a live fence of *Stachytarpheta* spp. (Verbenaceae) bushes, *Heliconia* spp. patches, and young secondary forest. The nest was collected on 18 April 2009 after the chicks fledged, and was deposited in the Museo de Zoología, Universidad de Costa Rica.

The nest was a cup built on a hanging portion of steel mesh under the elevated floor of the ranger station, 1 m above ground. The egg cup was 28.0 × 23.5 mm in diameter, and 15.8 ± 2.9 mm (mean ± SD) deep. The outside of the nest measured 37.1 × 40.7 mm in diameter and 19.7 ± 3.5 mm tall. The nest was comprised of two layers. The outer layer included tree bark, small pieces of dry leaves, twigs, spider web, and downy seeds (mostly Asteraceae). The inner layer was comprised mostly of dry fine plant fibers and downy plant material (Fig. 1).

The nest contained two completely feathered nestlings when found. The bills of the nestlings were black with reddish in the mandible base. The throat and breast of the nestlings were gray, and the backs were green with buffy-tipped feathers.

DISCUSSION

The nest structure, including the two-layer construction, is similar to nests described for other species of emeralds (Schuchmann 1999). However, the nest of Garden Emerald, unlike other emerald nests, contained no lichens, mosses, or fern materials (Oniki and Antunes 1998, Schuchmann 1999, Garrido and Kirkconnell 2000). The feather color pattern of the Garden Emerald nestlings was similar to that described for others emerald species where the nestlings

resemble the adult female plumage (Wolf 1964, Stiles and Skutch 1989, Schuchmann 1999).

The female did not attend the chicks during the night of 28 March, likely because the chicks filled the entire nest. We observed the female attending the nest and feeding both fledglings the following morning. The nest was built on an anthropogenic substrate, but we postulate that, in natural conditions, Garden Emeralds would build nests in the lower branches of bushes along trails, forest edge, or in forest gaps. Our observations reveal that Garden Emeralds can take advantage of human structures and successfully use them for nesting similar to wrens, swallows, or flycatchers (Stiles and Skutch 1989, Baicich and Harrison 2005, Sandoval and Barrantes 2009).

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The Nest of the Cipó Canastero (*Asthenes luizae*), an Endemic Furnariid from the Espinhaço Range, Southeastern Brazil

Henrique Belfort Gomes[1,3] and Marcos Rodrigues[2]

ABSTRACT.—The Cipó Canastero (*Asthenes luizae*) is a recently described species from the Espinhaço Range, southeastern Brazil. We describe the nest, eggs, and nestlings of this species. Six nests were found in four different territories, two of which were active. All nests were in *Vellozia nivea* (Velloziaceae). Mean measurements were: height above ground = 21.8 cm, entrance diameter = 4.3 cm, nest length = 23.5 cm, nest height = 23.3 cm, and nest width = 20.3 cm. Both active nests were parasitized by Shiny Cowbirds (*Molothrus bonariensis*). *Received 30 July 2008. Accepted 5 March 2010.*

The Cipó Canastero (*Asthenes luizae* Vielliard 1990; Furnariidae) is one of the four species of endemic birds of the Espinhaço Range (Vasconcelos 2008), an endemic bird area in South America (Stattersfield et al. 1998). Due to its restricted range and occurrence in a habitat subjected to significant anthropogenic (fire and cattle) and biological pressures (brood parasitism), this species has been classified globally as 'vulnerable' (Vielliard 1990, Collar et al. 1992, BirdLife International 2000). The recent discovery of the Cipó Canastero, an isolated *Asthenes* in southeastern Brazil, had great biogeographical significance, suggesting a historical relationship between the mountains of southeastern Brazil and the Andean-Chacoan-Pampean-Patagonian regions (Remsen 2003).

Anedoctal data regarding six nests of the Cipó Canastero were briefly discussed by Studer and Teixeira (1993). They reported one active nest with two eggs and five empty nests. The species is considered high priority for study and conservation due to its rarity, lack of biological data, and biogeographical importance (Stotz et al. 1996). Our objective is to provide detailed descriptions of the nest, eggs, and nestlings of the Cipó Canastero.

METHODS

Fieldwork was conducted at Alto da Boa Vista (19° 17′ S, 43° 35′ W), an area of rocky fields at an elevation of 1,230 to 1,355 m above sea level in the Serra do Cipó Range, District of Santana do Riacho, State of Minas Gerais, southeastern Brazil. The vegetation of the rocky fields is marked by sparse treelets and scrubs often with thick bark. Species of Velloziaceae, Eriocaulaceae, Compositae, Rubiaceae, and Orchidaceae are typical of rocky substrates in the area (Giulietti et al. 1997). This vegetation type is characterized by high floristic diversity and an elevated number of endemic and endangered plant species (Giulietti et al. 1997).

We randomly searched for nests in September-November 2005 within an area of ~100 ha where at least five pairs of adults had been daily observed vocalizing and foraging. The nests found were periodically monitored and their status recorded. We used calipers (0.05 mm precision) to measure the following parameters for each nest: length, height, and width of the nest, height above ground and entrance diameter (Fig. 1). Eggs were weighed with a 10 g spring balance (0.5 g scale), measured with calipers, and described regarding their format and color. We report mean ±SD for all varibles.

RESULTS

Six nests were found in four different territories, two of which were active and four were empty. Empty nests were found in territories with active nests. All nests were in 'canela-de-ema' shrubs (*Vellozia nivea*) and had a spherical or cylindrical shape (Fig. 1). The external part of the nests was built of sticks without thorns (15–55 cm in length), dry material of *Barbacenia* spp. (Velloziaceae) and *Vellozia* spp., and moss. The incubation chambers were covered by pilose material of a Cactaceae, feathers, dry fibers of

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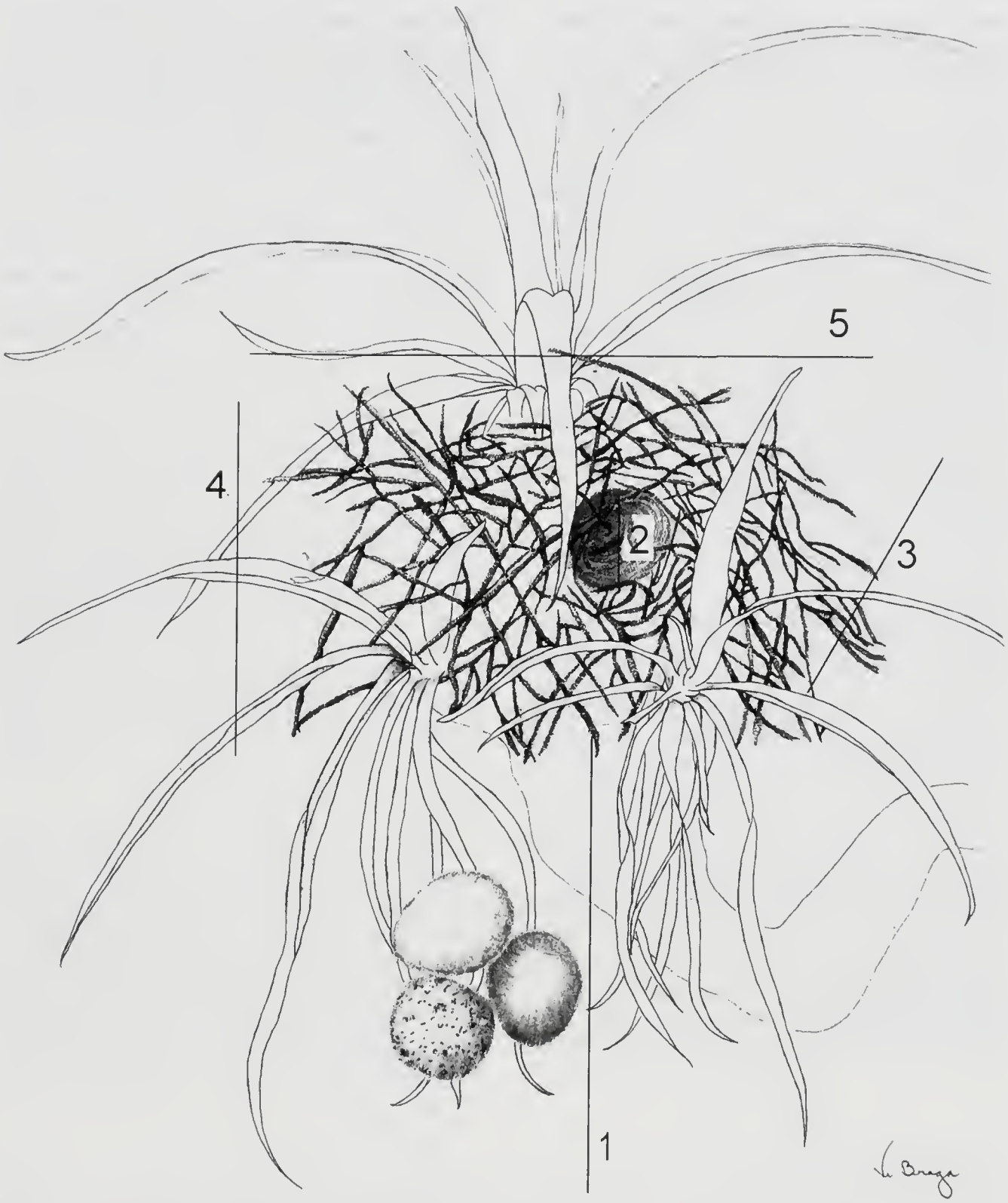

FIG. 1. Measurement points for nests of Cipó Canastero: (1) height above ground, (2) entrance diameter, (3) nest length, (4) nest height, and (5) nest width. Two white eggs of the Cipó Canastero and one of Shiny Cowbird are depicted below the nest.

Velloziaceae, and pilose material of a gall that develops in a shrub of *Erythroxylum* spp.

Nests were 21.8 ± 8.2 cm (n = 6) above ground and had an entrance diameter of 4.3 ± 0.5 cm (n = 4). Nest measurements were: length = 23.5 ± 4.3 by 20.3 ± 4.2 cm in width and a height of 23.3 ± 6.7 cm (n = 6). Both active nests were parasitized by Shiny Cowbirds (*Molothrus bonariensis*). One active nest had three eggs, one of Cipó Canastero and two of the cowbird, and the other had two Cipó Canastero eggs and one cowbird egg. The eggs of Cipó

Canastero were oval-shaped and completely white, while those of the cowbird varied in color from pink with brown stains, to blue with brown spots (Fig. 1). Cipó Canastero's eggs measured 21.8 ± 0.2 × 17.8 ± 0.1 mm and had a mass of 3 ± 0.5 g (n = 3).

One active nest was discovered on 21 September and was under construction. This nest had three eggs (Cipó Canastero = 1, Shiny Cowbird = 2) on 5 October. The Shiny Cowbirds eggs hatched between 10 and 12 days later. A nestling cowbird was found alive and the other was dead on 18 October, and the Cipó Canastero egg continued in the nest. This egg was found broken on 28 October, without development. The nestling cowbird was no longer in the nest on 2 November. Both adults were marked with colored rings at this nest. Only one individual Cipó Canastero was observed on the nest during incubation, and the other was next to the nest. Both adults were observed delivering food for the nestling cowbird.

The other active nest was found on 26 October and had three eggs (Cipó Canastero = 2, Shiny Cowbird = 1). The nest contained one cowbird nestling on 11 November and two nestlings of Cipó Canastero on 17 November. One nestling weighed 2.5 g and was 3.7 cm in length, and the other 2 g and 3.9 cm in length. The Cipó Canastero's nestlings had orange skin and yellowish beak and palate, and were covered with gray down. Both Cipó Canastero's nestlings had their eyes shut. The nestling Shiny Cowbird weighed 16 g on 17 November. Only the nestling Shiny Cowbird was in the nest on 20 November. The nestling Shiny Cowbird was not in the nest on 29 November and it was seen next to two adults about 150 m from the nest on 13 December.

DISCUSSION

The nests and eggs of Cipó Canastero we describe are similar to those briefly discussed by Studer and Teixeira (1993). These authors also found six nests of this species in *Vellozia nivea*. These findings suggest Cipó Canastero may specialize in using this plant species as a substrate for nesting. However, *V. nivea* does not occur in the entire range of the Cipó Canastero including the northern mountains in Minas Gerais, north of the Jequitinhonha River Valley (Vasconcelos 2008; R. Mello-Silva, pers. comm.). A possible explanation for occurrence of Cipó Canastero in areas where this plant is absent is that several other species of *Vellozia* are common and abundant in the rocky fields throughout the Espinhaço Range (Giulietti et al. 1997). Several other shrubs of different families, but with architecture similar to *V. nivea*, also occur in the rocky fields and it is possible that Cipó Canasteros also build their nests in them.

Zyskowski and Prum (1999) presented a phylogenetic analysis of nest architecture in Furnariidae. These authors had incomplete data about the nest of Cipó Canastero and they grouped this species in the same operational taxonomic unit as Canyon Canastero (*A. pudibunda*), Cactus Canastero (*A. cactorum*), Dusky-tailed Canastero (*A. humicola*), Rusty-vented Canastero (*A. dorbignyi*), Berlepsch's Canastero (*A. berlepschi*), Steinbach's Canastero (*A. steinbachi*), Short-billed Canastero (*A. baeri*), and Patagonian Canastero (*A. patagonica*). Nests of this group are characterized by their domed vegetative structure, built of sticks, and the presence of an entrance tunnel. The detailed nest description presented here supports this arrangement. However, it is possible that *Asthenes* is polyphyletic (Zyskowski and Prum 1999, Remsen 2003, Irestedt et al. 2006) and new analyses including the Cipó Canastero are needed to better understand the systematic position and the biogeographical affinities of this species (Vasconcelos et al. 2008).

Adult Shiny Cowbirds were observed around nests of Cipó Canastero at distances varying from 3 to 15 m. The Cipó Canastero seemed to ignore these species, but we observed a pair of Cipó Canastero chasing two individual Rufous-collared Sparrows (*Zonotrichia capensis*) that approached their nest. The lack of reaction of Cipó Canastero to presence of Shiny Cowbirds may suggest they do not recognize this species as a nest parasite.

The number of nests we found is low, but the presence of Shiny Cowbird eggs in the nests demonstrates the Cipó Canastero is a host. Shiny Cowbird eggs had a shorter hatching period, from 10 to 12 days for the first nest and 15–16 days in the second nest. This shorter hatching period allows Shiny Cowbird nestlings to develop sooner, providing them with higher chances of success. Early hatching in the first nest enabled the nestling of the parasite to make a hole in the egg of the host and, in the second, allowed the nestling cowbird (6.5 times larger in mass) to probably eject the Cipó Canastero nestlings from the nest or caused death by starvation.

Knowledge of the nesting substratum and reproductive period of species is fundamental for establishment of conservation programs. The Cipó Canastero remains common in Serra do Cipó, despite environmental impacts occurring during recent years within its area of occurrence (BirdLife International 2000). Nest records, however, are rare and more detailed studies on reproductive seasonality and factors related to the Cipó Canastero's success are needed to optimize the conservation of this threatened and restricted-range species.

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Nest Box Use by Great Tits in Semi–arid Rural Residential Gardens

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ABSTRACT.—We studied use of nest boxes by Great Tits (*Parus major*) in rural village gardens in a semi-arid area. Great Tits occupied 46.6% of the nest boxes, and used nest boxes within higher tree densities and with more tree species in the vicinity. Breeding success was greater in nest boxes with higher plant density, more plant species, and greater height of trees in the vicinity of the nest. The presence of children or dogs (*Canis lupus familiaris*) near nest boxes did not affect breeding parameters. Syrian Woodpeckers (*Dendrocopos syriacus*) enlarged 38.0% of nest box entrances during the first year. House Sparrows (*Passer domesticus*) occupied 41.0% of the nest boxes with enlarged holes and none of those with normal holes. Great Tits occupied both types, but significantly fewer pairs breeding in nest boxes with enlarged holes succeeded in fledging at least one young, probably due to their eviction by the larger House Sparrows. *Received 19 October 2009. Accepted 19 January 2010.*

Great Tits (*Parus major*) are one of the most studied passerines due to their wide distribution and use of nest boxes. Most studies have been in northern Europe (Sanz 1998) and, to a much lesser extent, in Mediterranean Europe (Beldal et al. 1998, Lambrechts et al. 2008), but rarely in the Middle East (Yavin 1987).

More studies have been of Great Tits breeding in deciduous (van Balen 1973, Riddington and Gosler 1995) and coniferous forests (Orell and Ojanen 1983, Mänd et al. 2005), than with those in suburban (Dhondt et al. 1984, Cowie and Hinsley 1987) and rural gardens (Perrins 1965, Riddington and Gosler 1995). Residential gardens around homes vary greatly in number of plant and tree species; studies in these locations facilitate a deeper understanding of the environmental factors birds use for nest site selection.

Great Tits in Mediterranean regions are the smallest species of cavity breeders and may lose nest sites to larger species, mainly House Sparrows (*Passer domesticus*) (Barba and Gil-Delgado 1990), unlike in Europe where Great Tits compete mainly with smaller species for nest sites and are the dominant species (Dhondt and Eykerman 1980, Minot 1981, Alatalo et al. 1986, Minot and Perrins 1986, Alatalo et al. 1987, Kempenaers and Dhondt 1991).

We studied nest box use by Great Tits in rural village gardens in a Mediterranean climate and examined environmental factors, in particular, the presence of children, dogs (*Canis lupus familiaris*), plants, trees, grass, and size of entrance holes of nest boxes, that may be related to occupation and breeding success of Great Tits.

METHODS

The study site was in Moshav Ram-On in the semi-arid Jezreel Valley, Israel (32° 31′ 55″ N, 35° 15′ 25″ E), 80–90 m above sea level with an average annual precipitation of 453 mm. The 50-ha study site comprised 170 houses, each with a garden of 500 m^2 and other small buildings used for storage. These were surrounded by agricultural areas, mainly fields of sweet corn, alfalfa, oats, wheat, grape vines, almond plantations, and olive groves.

Fifty-eight wood nest boxes (15 cm wide × 15 cm long × 24 cm high) with an entrance of 30 mm diameter, at a height of 1.5 to 2.0 m above the ground, were affixed during August 2006 to trees randomly with no more than one nest box per garden. Active nests (defined as a nest box in which Great Tits or House Sparrows built nests) were visited each week from 1 January 2007 to 1 June 2007. Laying date, clutch size, mean number of young per nest box after hatching, mean number of fledglings per laying (all pairs that laid at least 1 egg were included), and successful pairs (pairs that fledged at least 1 young) were recorded for each pair of Great Tits.

The following data were recorded for each nest box within a 30-m radius: presence of dogs (yes/no), presence of children (yes/no), plant density (rated 1 lowest to 5 highest, not including trees),

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TABLE 1. Characteristics ($\bar{x} \pm$ SE) of areas where Great Tits built nests in nest boxes in semi-arid rural gardens, 2007.

	Built nest		
	Yes	No	Mann-Whitney *U*
Plant density	3.04 ± 0.2 (n = 23)	2.74 ± 0.2 (n = 23)	U = 230.0, n = 46, P = 0.43
Tree density	3.26 ± 0.2 (n = 23)	2.43 ± 0.2 (n = 23)	U = 164.5, n = 46, $P < 0.05$
Number of grass species	0.94 ± 0.1 (n = 18)	1.00 ± 0.0 (n = 19)	U = 161.5, n = 37, P = 0.30
Number of tree species	3.96 ± 0.5 (n = 23)	2.26 ± 0.3 (n = 23)	U = 152.5, n = 46, $P < 0.05$
Number of plant species	6.17 ± 1.4 (n = 23)	4.55 ± 0.6 (n = 22)	U = 228.0, n = 45, P = 0.57
Height of trees	3.65 ± 0.4 (n = 23)	2.96 ± 0.3 (n = 23)	U = 184.5, n = 46, P = 0.07
Distance from homes	3.45 ± 0.3 (n = 22)	3.52 ± 0.3 (n = 23)	U = 284.5, n = 46, P = 0.91
Distance closest neighboring nest box	4.04 ± 0.3 (n = 23)	3.57 ± 0.3 (n = 23)	U = 212.5, n = 46, P = 0.23
Distance to street	3.50 ± 0.4 (n = 22)	2.61 ± 0.4 (n = 23)	U = 186.5, n = 45, P = 0.11

tree density (1 to 5), number of grass species, number of tree species, number of plant species, height of trees (1 to 5), distance from the house (1 to 5), distance to closest neighboring nest box (1 to 5), distance to street (1 to 5), and whether the entrance hole had been enlarged by Syrian Woodpeckers (*Dendrocopos syriacus*) (yes/no). Plant density, tree density, height of trees, distance from the house, distance to closest neighboring nest box, and distance to street were also rated.

All statistical tests were two-tailed and all tests were non-parametric. Descriptive breeding data were analyzed using the Mann-Whitney *U*-test. Spearman's test was used to analyze rank correlations among breeding parameters. Chi-square and Fisher's exact tests were used for comparing rate of occupation and nest success, between nests of different entrance sizes, and nest boxes within the vicinity of dogs and/or children. Levels of significance were set at $P < 0.05$. Statistical analyses were performed using Statistica (Version 7.1) software and SPSS (Version 17).

RESULTS

Great Tits built nests in 46.6% of the nest boxes (n = 58), and laid eggs in 85.2% (n = 27) of these. They succeeded in fledging at least one young in 74.1% of the nest boxes in which they laid eggs (n = 20). The mean laying date was 20 March 2007 (n = 23, SE 0.2), mean (± SE) clutch size was 7.13 ± 0.4 (n = 15), mean number of fledglings per laying pair was 4.9 ± 0.6 (n = 23), and mean number of fledglings per successful pair was 5.7 ± 0.4 (n = 20). The breeding density was 5.4 pairs/10 ha.

Great Tits built more nests in nest boxes that were in an area with higher tree density and a higher number of tree species, but no differences were found between nest box location and other habitat attributes (Table 1). Greater breeding success was observed (fledged at least 1 nestling) in nest boxes in the vicinity of higher plant density, more plant species, and greater height of trees (Table 2). Clutch size was not correlated with nest box location or any habitat attribute; number of Great Tit fledglings was negatively correlated with tree height in the vicinity of nests (Table 3).

The presence of dogs did not affect clutch size (Mann- Whitney U = 4.0, n = 8, P = 0.38), number of fledglings (Mann-Whitney U = 22.0, n = 15, P = 0.55), or rate of occupation of nest boxes (χ^2 = 0.04, n = 30, P = 0.92). The presence of children also did not affect Great Tit clutch size (Mann-Whitney U = 16.0, n = 14, P = 0.57), number of fledglings (Mann-Whitney U = 28.0, n = 18, P = 0.33) or rate of occupation of nest boxes (χ^2 = 0.46, n = 44, P = 0.46).

Syrian Woodpeckers enlarged 38.0% of nest box (n = 58) entrances during the first year. Great Tits equally occupied nest boxes with both enlarged and normal hole entrances (χ^2 = 0.16, n = 58, P = 0.69), but significantly fewer pairs breeding in nest boxes with enlarged holes succeeded in fledging at least one young (Fig. 1). House Sparrows occupied 41.0% of the nest boxes with enlarged entrance holes and none with normal holes (Fig. 1).

DISCUSSION

Differences in occupation and breeding success varied with local habitat attributes around the nest box even though 46.6% of the nest boxes overall were occupied by Great Tits. Tree number/density/height and plant number/density had a

TABLE 2. Characteristics ($\bar{x} \pm$ SE) of areas that affected nest success of Great Tits fledging at least 1 young per nest in nest boxes in semi-arid rural gardens, 2007.

	Succeeded to fledge young		
	Yes	No	Mann-Whitney *U*
Plant density	3.35 ± 0.3 (n = 17)	2.17 ± 0.3 (n = 6)	U = 23.0, n = 23, $P < 0.05$
Tree density	3.47 ± 0.3 (n = 17)	2.67 ± 0.4 (n = 6)	U = 32.5, n = 23, $P = 0.18$
Number of grass species	0.93 ± 0.1 (n = 14)	1.00 ± 0.0 (n = 6)	U = 26.0, n = 18, $P = 0.60$
Number of tree species	4.47 ± 0.7 (n = 17)	2.50 ± 0.4 (n = 6)	U = 26.5, n = 23, $P = 0.08$
Number of plant species	7.53 ± 1.7 (n = 17)	2.33 ± 0.6 (n = 6)	U = 10.0, n = 23, $P < 0.01$
Height of trees	3.18 ± 0.2 (n = 17)	5.00 ± 0.0 (n = 6)	U = 3.0, n = 23, $P < 0.001$
Distance from homes	3.25 ± 0.4 (n = 16)	4.00 ± 0.6 (n = 6)	U = 36.0, n = 22, $P = 0.34$
Distance closest neighboring nest box	4.12 ± 0.3 (n = 17)	3.83 ± 0.5 (n = 6)	U = 44.5, n = 23, $P = 0.62$
Distance to street	3.69 ± 0.4 (n = 16)	3.00 ± 0.9 (n = 6)	U = 40.5, n = 22, $P = 0.56$

role in nest selection and success of breeding pairs. Trees are important for Great Tits, as their reproductive parameters increase in accordance with size of the woodland (Hinsley et al. 1999). Nestling diet in woodlands contained more caterpillars (the preferred prey of Great Tits) than in marginal habitats with fewer and younger trees (Riddington and Gosler 1995). Children, dogs, and proximity to streets did not appear to affect Great Tit breeding. In contrast, Park et al. (2005) found a difference in breeding near streets. Diet was not monitored in the present study but may be important, as both tree and plant densities may influence prey abundance. Gardens with a higher abundance of plants and trees are normally irrigated more, providing green leaves for caterpillars.

Breeding densities and success were within the range of other studies in gardens (Dhontdt et al. 1984, Cowie and Hinsley 1987), but lower than for pairs in deciduous forests (Cowie and Hinsley 1987). Clutch size was smaller than in most studies in Europe, and fits within the quadratic relation suggested by Sanz (1998).

Syrian Woodpeckers were the primary cavity builders in the study site and, in some cases, enlarged natural cavities that were too small for them but which were used by Great Tits. Consequently, the enlarged entrances become available for larger species including House Sparrows. Great Tit and House Sparrow diets do not overlap, but both use cavities and may compete for them. House Sparrows in our study occupied 41.0% of the nest boxes with enlarged holes and none with normal holes. Great Tits occupied nest boxes with both enlarged and normal hole entrances similarly, but significantly fewer pairs breeding in nest boxes with enlarged holes succeeded in fledgling at least one young, most likely due to their eviction by larger House Sparrows.

Barba and Gil-Delgado (1990) reported Great Tits occupied a diminishing number of nest boxes over a period of 3 years and suggested this was

TABLE 3. The relation between habitat attributes, clutch size, and number of fledglings in semi-arid rural gardens, 2007.

	Clutch size[a]	Number of fledglings[a]
Plant density	$r = -0.12$, n = 12, $P = 0.71$	$r = 0.10$, n = 20, $P = 0.67$
Tree density	$r = -0.22$, n = 12, $P = 0.50$	$r = 0.07$, n = 20, $P = 0.76$
Number of grass species	$r = -0.51$, n = 8, $P = 0.19$	$r = -0.35$, n = 15, $P = 0.21$
Number of tree species	$r = -0.14$, n = 12, $P = 0.66$	$r = 0.10$, n = 20, $P = 0.69$
Number of plant species	$r = 0.29$, n = 12, $P = 0.37$	$r = 0.23$, n = 20, $P = 0.34$
Height of trees	$r = -0.31$, n = 12, $P = 0.32$	$r = -0.51$, n = 20, $P < 0.05$
Distance from homes	$r = 0.28$, n = 12, $P = 0.38$	$r = 0.14$, n = 19, $P = 0.56$
Distance closest neighboring nest box	$r = -0.02$, n = 12, $P = 0.96$	$r = 0.19$, n = 20, $P = 0.41$
Distance to street	$r = -0.57$, n = 12, $P = 0.054$	$r = 0.01$, n = 19, $P = 0.97$

[a] Spearman's test.

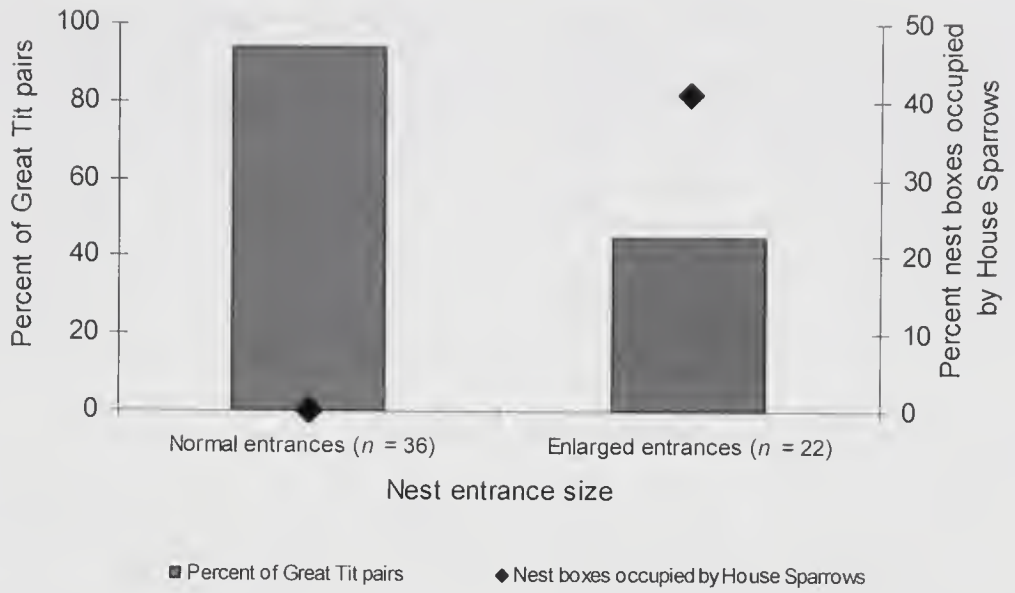

FIG. 1. Percent of Great Tit pairs that succeeded in fledging young ($\chi^2 = 7.92$, $n = 27$, $P < 0.01$) and percent nest boxes occupied by House Sparrows ($\chi^2 = 13.91$, $n = 58$, $P < 0.001$) from nest boxes with normal entrance hole (30 mm) and with entrance holes enlarged by Syrian Woodpeckers.

due to an increase in House Sparrows and black rats (*Rattus rattus*) in the nest boxes. The normal entrance holes in our study prevented House Sparrows from entering and Great Tits were able to breed, whereas in the entrances that were enlarged, sparrows also were able to enter. Both this study and that of Barba and Gil-Delgado (1990) suggest that competition may be the reason for decreased occupation (Barba and Gil-Delgado 1990) and breeding success (this study), but both studies were purely observational. Experimental studies manipulating hole entrance size are needed to better understand whether competition between the two species affects their breeding success.

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Analysis of Nest Sites of the Resplendent Quetzal (*Pharomachrus mocinno*): Relationship between Nest and Snag Heights

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ABSTRACT.—The Resplendent Quetzal (*Pharomachrus mocinno*) is of particular conservation concern because of its iconic status in Central American culture. This species is a secondary cavity nester and modifies abandoned woodpecker nest sites in dead tree trunks (i.e., snags). We used 11 historical nest sites, reported in 1969, from Atitlan, Guatemala and 10 recent nest sites from San Gerardo de Dota, Costa Rica to examine if a relationship exists between nest and snag height. There were significant differences between Costa Rica and Guatemala in both nest height (6.3 vs. 10 m, respectively; $t\text{-test}_{14} = -2.49$, $P = 0.042$) and snag height (8.1 vs. 14.0 m, respectively; $t\text{-test}_{13} = -2.39$, $P = 0.033$). There was no difference in nest heights relative to snag heights for Costa Rica (0.76) and Guatemala (0.77; $t\text{-test}_{17} = -0.20$, $P = 0.84$). One aspect of conservation efforts for this species has been placement of nest boxes to provide nesting sites for additional pairs. Our results provide a better understanding of placement requirements for nest boxes to encourage their use anywhere within the range of the species. *Received 3 December 2009. Accepted 5 April 2010.*

Cavity nesting-species have challenges from finding the limited resource of a nest cavity (Cornelius et al. 2008) to predation events on eggs, chicks, or adults (Martin and Li 1992, Brightsmith 2005). Many cavity-nesting species in both temperate and tropical latitudes display preferences for cavity height in relation to height of the tree or snag (i.e., relative nest height). Primary cavity-nesting species, including Red-headed Woodpecker (*Melanerpes erythrocephalus*), Northern Flicker (*Colaptes auratus*), and Acorn Woodpecker (*M. formicivorus*), place nests at relative nest heights of 0.49–0.58 (Sedgwick and Knopf 1990, Hooge et al. 1999). Some secondary-cavity nesters in the temperate zone select relative nest heights with more variation: Black-capped Chickadees (*Poecile atricapillus*) and House Wren (*Troglodytes aedon*) at 0.37–0.38, European Starlings (*Sturnus vulgaris*) and American Kestrels (*Falco sparverius*) at 0.5 (Sedgwick and Knopf 1990), and Eastern Screech-Owls (*Megascops asio*) at 0.31 (Belthoff and Ritchison 1990).

Less information is available in tropical areas about selection of relative nest heights by secondary-cavity nesters. The Resplendent Quetzal (*Pharomachrus mocinno*) is an exclusive secondary-cavity nester (Johnsgard 2000) that, as an iconic species, has become the focus of conservation efforts at many locations throughout Central America. More efficient planning and implementation has occurred with concomitant conservation benefits for many other species in focusing on one vulnerable and highly mobile species (Wheelwright 1983, Powell and Bjork 1995). The Resplendent Quetzal throughout its range uses natural cavities created from stubs of fallen branches or abandoned nest cavities of other species, primarily woodpeckers, which

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Resplendent Quetzals occupy and enlarge (Wheelwright 1983). The Acorn Woodpecker is the primary excavator in the Talamanca Mountain Range of southern Costa Rica. This species excavates several locations for nesting and then abandons these sites as the level of decay increases (Koenig et al. 1995). We examined nest heights of currently active (in Costa Rica) and historical (in Guatemala; Bowes and Allen 1969) Resplendent Quetzal nests and compared them to heights of snags where they occur. We sought to ascertain if there were: (1) any differences in nest placement between countries, (2) consistent relative nest heights for Resplendent Quetzals, and (3) any implications for future conservation efforts.

METHODS

Study Site.—The San Gerardo de Dota Valley is on the Pacific Slope of the Talamanca Mountain Range, 85 km southeast of San Jose below the Cerro del Muerte on the Pan-American highway. The Quetzal Education Research Center (QERC; 9° 33′ 08.67″ N, 83° 48′ 23.18″ W; 2,200 m asl) is part of a 400-ha preserve consisting of homesteads pioneered in 1952 for dairy farming. Much of the pasture land was converted to fruit-tree orchards starting in 1984 and the last pasture areas were allowed to begin the process of succession to forest in 1996 (Neuenschwander 2001). The primary forest is dominated by oaks (*Quercus* spp.) with an understory dominated by Lauracea, Moracea, and Fabacea. Secondary forest areas have similar composition. The Savegre River bisects the valley and most human activity occurs in the associated riparian area. This area has been planted with eucalyptus (*Eucalyptus* spp.) trees for erosion control to supplement the remaining native species.

Data Collection.—Our initial search for both active and past nests from January through April 2008 involved interviewing local guides and individuals in San Gerardo de Dota, Costa Rica who were familiar with nest locations. We searched along established trails to locate these and other nests. Eight of the 10 sites that we located were active and two were not being used although observations in previous years indicated these were active nest sites. We observed pair activity including exchange of occupancy or delivery of food items at a site to document it was active. We measured nest and snag height using a standard metric tape measure and clinometer (Suunto PM-5). We calculated relative nest height as the height of the nest divided by the height of the snag. This calculation was also done for the 11 reported sites from Guatemala (Bowes and Allen 1969). We used 21 nest sites for analysis, 10 from Costa Rica and 11 sites in Guatemala reported by Bowes and Allen (1969). All 21 sites were in trunks of dead trees (i.e., snags).

Statistical Analysis.—We had unequal number of sites in each country and a recognized difference in subspecies. Thus, we used two-sample *t*-tests assuming unequal variance to compare nest and snag heights, and the ratios between countries (Van Emden 2008). We used Pearson product-moment correlation to examine if the nest-to-snag relationship was linear across sites. We used Systat 11 (Systat 2004) for all of our calculations.

RESULTS

There was only one Resplendent Quetzal nest cavity per tree at each Costa Rica site. There were many woodpecker holes in a snag, but the majority, based on shape and depth, were relic foraging holes. There were two additional large holes in the case of tree # 4; one was 1 m above the active nest while the other was 650 cm below it facing a different direction. Tree # 2 had one hole 500 cm above the nest that was used by Spot-crowned Woodcreepers (*Lepidocolaptes affinis*). Nesting success was difficult to ascertain and it remains unclear how many nest sites were successful. However, we observed a nestling that left nest # 1 prematurely and died, and that nest # 5 was abandoned by the adults prior to fledging.

Snag heights in Costa Rica averaged 8.1 m (s = 2.78, range = 1.9–10.8 m, n = 10) and were lower than those used in Guatemala, where the average was 14.0 m (s = 7.57, range = 5.8–29.0 m, n = 11; $t\text{-test}_{13} = -2.39$, $P = 0.033$). The average nest height of snags used in Costa Rica (6.3 m, s = 2.53, range = 1.4–10.1 m, n = 10) was also lower than in Guatemala (10.8 m, s = 6.15, range = 4.0–24.4 m, n = 11; $t\text{-test}_{14} = -2.49$, $P = 0.042$). The product-moment correlation between snag height and nest height was high ($r = 0.976$, $P < 0.0001$; Fig. 1). No difference was found in nest heights relative to snag heights for Guatemala (0.77) and Costa Rica (0.76; $t\text{-test}_{17} = -0.20$, $P = 0.84$).

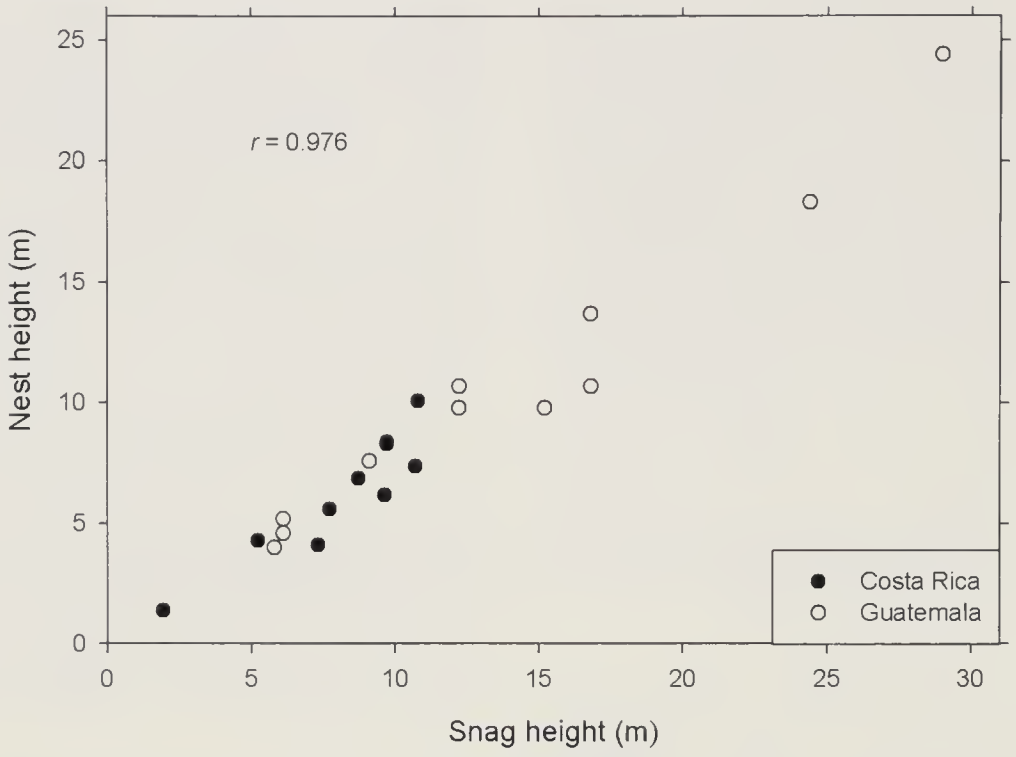

FIG. 1. Relationship of snag versus nest height of Resplendent Quetzals in two populations in Costa Rica and Guatemala ($r = 0.976$, $P < 0.0001$).

DISCUSSION

Successful nesting by Resplendent Quetzals is dependent on numerous factors; from males having sufficient covert lengths and display flights (Unger 1988) to defending and provisioning chicks. One aspect that is crucial to successful nesting is finding suitable cavities. Resplendent Quetzals in the northern portion of their range excavate entire nests as there are no woodpeckers or their allies that produce a cavity of suitable size (Renner 2005). We observed Resplendent Quetzals at San Gerardo de Dota making small holes in dead trees prior to mating, but nest cavities were developed from cavities initially excavated by Acorn Woodpeckers. The difference may be related to most nest sites at San Gerardo de Dota being in trunks of oaks, which have relatively hard wood.

Finding abandoned Acorn Woodpecker nests appears to be important, but relative nest height may be of primary importance in selecting a nest site. Average relative nest height was 0.65 (Renner 2005) when no previously excavated cavities were available, primarily due to a lack of sufficiently large woodpecker species. Average relative nest heights were 0.76 and 0.77, respectively in our study and the earlier study in Guatemala (Bowes and Allen 1969). Both our Costa Rica site and the Guatemala (Bowes and Allen 1969) site are within the range of a woodpecker species that is sufficiently large to excavate a cavity that may then be enlarged by the Resplendent Quetzal (Skutch 1944, Bowes and Allen 1969, Johnsgard 2000).

The primary-cavity nester at San Gerardo de Dota is the Acorn Woodpecker. This species nests roughly half way up in a snag (Hooge et al. 1999). As the snag ages, material is lost from the top reducing the overall relative nest height. It is only after sufficient decay that the site is abandoned by woodpeckers and becomes available for Resplendent Quetzals. Nests are often used by Resplendent Quetzals for several years until the snag finally collapses.

The continued presence of Resplendent Quetzals is of primary interest to the inhabitants of San Gerardo de Dota as there are more than 12,000 visitors annually to the Quetzal Education Research Center. Conservation efforts at numerous locations throughout the range of the Resplendent Quetzal have included addition of artificial nest boxes (Bowes and Allen 1969, LaBastille 1974). Approximately four nest boxes per year, including replacements, have been in place since 1993 at San Gerardo de Dota. These boxes potentially could provide nesting sites for additional pairs, but none has been used. Thus, there may be sufficient numbers of natural sites for the number of nesting pairs. However, it is possible the

existing boxes are inappropriately positioned. These boxes are mounted at the top of 2.5 m posts, which do not extend above the boxes like the snags above the natural nesting cavities. Further, the absolute height of the nest boxes is considerably below the average heights of natural nesting cavities recorded in our study.

Conservation efforts for the Resplendent Quetzal have implications for many other species in the tropical cloud forests of Central America following succession, which provides new areas for nesting. Completion of the proposed Meso-American biological corridor in this area could be beneficial for Resplendent Quetzals and other species (Kaiser 2001).

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Parasitism of a Blue-winged Teal Nest by a Northern Shoveler in South Dakota

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ABSTRACT.—Nest parasitism in dabbling ducks is uncommon. Northern Shovelers (*Anas clypeata*) are considered infrequent parasites and Blue-winged Teal (*A. discors*) are rarely hosts to nest parasitism. We documented parasitism of a Blue-winged Teal nest by a Northern Shoveler. We reviewed 3,003 records from nests located in 1994 to 1997 in North Dakota and documented only one duck nest parasitized by a Northern Shoveler. Only nine of 1,494 Blue-winged Teal nests were parasitized. We found no evidence of Northern Shovelers parasitizing Blue-winged Teal nests in our nest records and only one account in the literature. *Received 12 January 2010. Accepted 24 March 2010.*

Northern Shovelers (*Anas clypeata*) and Blue-winged Teal (*A. discors*) are common upland nesting ducks in the northcentral United States and prairie Canada (Dubowy 1996, Rohwer et al. 2002). The estimated abundance of Northern Shoveler and Blue-winged Teal in the traditional survey area was well above the long-term average in 2009 (USDI 2009).

Nest parasitism occurs when a female purposely lays eggs in a nest to be raised by an individual that is not her mate (Sayler 1992). Nest parasitism is relatively uncommon among dabbling ducks, except for cavity nesting or ducks that crowd together on nesting islands (Sayler 1992). Northern Shovelers are documented to parasitize nests of other ducks (Glover 1956, Weller 1959, Sayler 1992, Zimmerman et al. 2003). Blue-winged Teal nests may rarely be parasitized by other ducks, but documentation is lacking (Rohwer et al. 2002). We document the second reported case of a Northern Shoveler parasitizing a Blue-winged Teal nest.

OBSERVATIONS

We flushed a Northern Shoveler hen from a nest on the morning of 12 May 2009. The nest was in 0.3-m high grass, ~0.4 m from a gravel railroad right-of-way and 20 m from a wetland near Aberdeen, South Dakota (45° 27′ 28″ N, 98° 24′ 58″ W). Examination of the nest revealed two small (~46–49 mm) and two medium (~52–55 mm) eggs. The small eggs were tan in color and the medium eggs were olive-tan and lighter in color. During later visits the nest contained four small and four medium eggs on 14 May 2009, six small and four medium eggs on 16 May 2009, and seven small and four medium eggs on 17 May 2009. A hen Blue-winged Teal flushed from the nest on 17 May 2009 during our approach and down and breast feathers diagnostic of the species had been added to the nest. The ultimate fate of the nest could not be ascertained due to the temporary nature of our visit in South Dakota.

DISCUSSION

Northern Shoveler eggs are described as pale olive-buff to a pale greenish gray in color (Bent 1923b, Palmer et al. 1976b, Bellrose 1980). Average length for Northern Shoveler eggs ranges from 52.2 to 52.85 mm (Bent 1923b, Palmer et al. 1976b, Dubowy 1996). Blue-winged Teal eggs are reported as light buff-tan (Bennett 1938), creamy tan (Glover 1956, Palmer et al. 1976a), or cream (Rohwer et al. 2002) in color and average length ranges from 46.4 to 47.1 mm (Bent 1923a, Glover 1956, Palmer et al. 1976a). The color and length of the eggs we observed suggests the medium eggs belonged to Northern Shoveler and the small eggs to Blue-winged Teal. Broley (1950) describes Blue-winged Teal down feathers with conspicuous white centers and dark tips and breast feathers with an elongated dark sub-terminal area and light proximal portion. Feathers in our nest matched this description. Observation of the hen Northern Shoveler on 12 May 2009, the hen Blue-winged Teal and feathers in the nest on 17 May 2009, along with the egg differences strongly suggests the Northern Shoveler parasitized the nest of the Blue-winged Teal.

Blue-winged Teal prefer nesting in upland sites (Bent 1923a, Bennett 1938, Glover 1956, Johns-

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gard 1975, Palmer et al. 1976a, Bellrose 1980). Rohwer et al. (2002) reported Blue-winged Teal rarely nest in high densities on islands or on muskrat (*Ondatra zibethicus*) houses and nests are dispersed, not readily accessible, and nest parasitism is rare, but documentation is lacking. Bent (1923a) described an account of a Blue-winged Teal nest containing four eggs of the teal and five eggs of another duck species. Bellrose (1980) included Blue-winged Teal as victims of Redhead (*Aythya americana*) parasitism. Lokemoen (1991) reported that Blue-winged Teal nests had parasitism in eight of 13 nests on islands, but zero of 54 nests on peninsulas. Zimmerman et al. (2003) found Blue-winged Teal nests parasitized at rates from 24 to 72% over a 7-year period on small islands in North Dakota. Glover (1956) reported only one of 186 Blue-winged Teal nests examined was parasitized by another duck which was a Northern Shoveler.

We examined data for 3,003 nests collected as described by the Northern Prairie Wildlife Research Center (1993) that we visited in northcentral North Dakota from May to July 1994–1996 (Garrettson and Rohwer 2001). Of these nests, 1,494 were Blue-winged Teal and only nine (0.6%) were reported as parasitized. None was parasitized by a Northern Shoveler. We found only one case of Northern Shoveler parasitism, and egg morphology and color suggested conspecific parasitism (1 of 129 Northern Shoveler nests).

Weller (1959) listed parasitic egg-laying by Northern Shoveler in nests of Mallard (*Anas platyrhynchos*), American Wigeon (*A. americana*), Cinnamon Teal (*A. cyanoptera*), and Redhead. Fournier and Hines (2001) found two of 669 scaup nests parasitized by Northern Shovelers. Zimmerman et al. (2003) reported Northern Shovelers parasitized three of 1,642 nests, but did not identify the parasitized species. Only Glover (1956) reported parasitic egg-laying by a shoveler in the nest of a Blue-winged Teal. Considering the abundance of these species and overlap in breeding range and nesting habitat, it is surprising that parasitism of Blue-winged Teal nests by Northern Shovelers is so rarely reported.

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Nest Predators of Ground-nesting Birds in Montane Forest of the Santa Catalina Mountains, Arizona

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ABSTRACT.—We used time-lapse video cameras and track plates to identify nest predators of Red-faced Warblers (*Cardellina rubrifrons*) and Yellow-eyed Juncos (*Junco phaeonotus*) in high-elevation (> 2,300 m) forests of the Santa Catalina Mountains in southeastern Arizona. Mammals, especially gray fox (*Urocyon cinereoargenteus*) and cliff chipmunk (*Tamias dorsalis*), were the principal nest predators of Red-faced Warblers and Yellow-eyed Juncos within our study system, accounting for 89% of all nest depredations. Our study is one of the first to use video cameras at real nests to document the prevalence of nest predators in montane forest ecosystems. Additional research is needed to learn if mammals are the dominant nest predators in other montane environments. *Received 23 October 2009. Accepted 24 March 2010.*

Nest depredation is the most common cause of reproductive failure of small land birds (Ricklefs 1969, Martin 1992). However, we lack reliable data on the identity and relative importance of nest predator species for most birds (Thompson 2007). Information on nest predators is particularly sparse for birds that breed in high-elevation (>2,300 m) forests in sky island mountain ranges of the southwestern United States. For example, ≥89% of nest failures of ground-nesting birds in high-elevation forests of the Santa Catalina Mountains in southeastern Arizona is attributed to nest depredation (Kirkpatrick and Conway 2010). However, the identity of even the most common nest predators remains unknown. Identification of nest predators is a critical first step in managing breeding populations of birds and in discerning how nest depredation shapes nest-site selection, life history strategies, and breeding behavior in birds (Weatherhead and Blouin-Demers 2004, Thompson 2007).

We used time-lapse video cameras (henceforth "video cameras") to monitor nests of Red-faced Warblers (*Cardellina rubrifrons*) and Yellow-eyed Juncos (*Junco phaeonotus*) in montane forests of the Santa Catalina Mountains in southeastern Arizona. Use of video cameras to monitor bird nests provides a reliable method to identify common nest predators (McQuillen and Brewer 2000, Williams and Wood 2002), but the technology is expensive and labor intensive and often only a small sample of nests can be monitored (Thompson 2007). We augmented video camera monitoring with track plates (Wilson and Delahay 2001) to identify potential nest predator species within our study system.

METHODS

Study Area.—We conducted research in five 16–20 ha study plots (2,300–2,800 m elevation) within several forested drainages (Kirkpatrick and Conway 2010) and one forested ridge (Kirkpatrick and Conway 2005) in the Santa Catalina Mountains, Pima County, Arizona, USA. Temperatures within our study area varied from an average of 6.5° C in mid-April to an average of 17.6° C in mid-July (Decker and Conway 2009).

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Nest Monitoring.—We searched for and monitored nests of Red-faced Warblers and Yellow-eyed Juncos in our five study plots from late April to mid-July in 2005–2006. Red-faced warblers and Yellow-eyed Juncos are the two most common ground-nesting birds within our study area: they breed concurrently, share similar nest-site characteristics, and nest in close association (Kirkpatrick and Conway 2010). Thus, we were reasonably confident that nests of both species would be susceptible to the same community of nest predators.

Video Cameras.—We monitored 16 Red-faced Warbler and 23 Yellow-eyed Junco nests with continuously-operated, time-lapse (5 frames/sec), video cameras equipped with infrared illumination for night-time photography (Fieldcam TLV, Fuhrman Diversified Inc., Seabrook, TX, USA; McQuillen and Brewer 2000). The nesting stage at which we first set out video cameras at nests varied: building (19% of nests), egg laying (12%), incubation (54%), and nestling (15%). We attached a small (5 × 2 × 2 cm) camera via a small articulated arm to a small wooden stake buried in the ground ~ 1 m from the nest and positioned the camera so that it was 40–60 cm from the nest. We concealed the camera and its articulated arm with camouflage fabric and ran a cable (hidden under leaf litter) > 15 m from the video camera to a concealed location where we placed the video recorder and battery.

We visited each video recorder every 24 hrs to change video tapes and batteries, and to check the status of the nest remotely with a hand-held video monitor. We occasionally approached nests along a defined trail to verify nest contents or to adjust cameras. We made no effort to mask our scent trail during these nest checks. Human scent trails leading to artificial ground nests in our study area did not increase the probability of nest depredation (Kirkpatrick and Conway 2009). We left video cameras at nests until young fledged or nests failed; we then reviewed video tapes of all depredated nests to identify the species of nest predator and the date and time of each depredation event. We assumed that multiple visits to a nest by the same predator species were the result of a single individual of that species.

Track Plates.—We placed 38 track plates at 100-m intervals along the center of four of our five study plots during the middle of the bird breeding season (3 Jun 2007), alternating locations of the track plates from one side of the drainage to the other. We placed the plates on relatively flat ground at a random distance <50 m from the drainage bottom ($\bar{x} \pm$ SD: 26 ± 10 m). We chose a 50-m distance interval because Red-faced Warblers and Yellow-eyed Juncos select nest sites that average 26 and 21 m, respectively, from drainage bottoms within our study area (Kirkpatrick and Conway 2010).

We used a protocol similar to Cain (2001) to construct track plates from galvanized steel sheeting (60 × 91 cm) and taped a piece of contact paper (30 × 46 cm) to the middle of each plate. We sprayed a mixture containing two parts isopropyl alcohol and one part blue carpenter's chalk (Drennan et al. 1998) on the track plate around the contact paper and placed a Japanese Quail (*Coturnix japonica*) egg covered in chicken (*Gallus gallus*) egg yolk on the center of the contact paper. We calculated an index of predator activity based on the percentage of the 38 track plates that had ≥1 identifiable track of a predator species following a 6-day exposure period (Drennan et al. 1998).

RESULTS

Video Cameras.—Nineteen of 39 nests with video cameras were successful, 17 were depredated (total of 18 depredation events; Table 1), two were abandoned due to inclement weather, and one was abandoned for an unknown reason. Both Red-faced Warbler and Yellow-eyed Junco nests were depredated by gray foxes (*Urocyon cinereoargenteus*), cliff chipmunks (*Tamias dorsalis*), and Steller's Jays (*Cyanocitta stelleri*). One Yellow-eyed Junco nest was depredated partially by a gray fox and a woodrat (likely *Neotoma mexicana*). Gray foxes and the woodrat depredated nests at night (67% of all nest depredation events), whereas cliff chipmunks and Steller's Jays depredated nests during the day (33% of all nest depredation events; Table 1). Gray foxes depredated video camera nests both early and later in the avian breeding season (27 Apr–19 Jul), whereas cliff chipmunks depredated video camera nests only later in the season (1 Jun–1 Jul).

Track Plates.—We identified tracks of six mammal and one bird species on track plates in early June 2007. Indices of predator activity were 50% for gray fox, 32% for mice (*Peromyscus* spp.), 32% for cliff chipmunk, 8% for Abert's squirrel (*Sciurus aberti*), 5% for Steller's Jay, 3% for bobcat (*Lynx rufus*), and 3% for domestic dog (*Canis lupus familiaris*). Pilot work using track

TABLE 1. Depredation events at Red-faced Warbler and Yellow-eyed Junco video camera nests by four nest predator species in high-elevation (>2,300 m) forest within the Santa Catalina Mountains, Arizona (late Apr to mid Jul, 2005–2006).

Nest predator	Depredation events			Time range (hrs) of depredations[a]
	Red-faced Warbler nests	Yellow-eyed Junco nests	Totals	
Gray fox	3	8	11	2004–0330
Cliff chipmunk	2	2	4	0645–1911
Steller's Jay	1	1	2	0800–1551
Woodrat[b]	0	1	1	0200–0420[c]
Totals	6	12	18	

[a] Mountain Standard Time.
[b] Likely *N. mexicana* (Kirkpatrick and Conway 2006).
[c] A woodrat depredated the brooding female Yellow-eyed Junco at 0200 hrs and then returned to the nest to depredate one of three nestlings at 0420 hrs. A gray fox depredated the two remaining nestlings (which were still alive) at 0218 hrs the next day (Kirkpatrick and Conway 2006).

plates in early May 2007 also recorded rock squirrel (*Spermophilus variegatus*) and Common Raven (*Corvus corax*) within our study area (C. Kirkpatrick, unpubl. data).

DISCUSSION

Mammals, especially gray fox and cliff chipmunk, were the principal predators of Red-faced Warbler and Yellow-eyed Junco nests within our study system, accounting for 89% of all nest depredations documented on video. Gray fox and cliff chipmunk are common in montane forests throughout southeastern Arizona (Hoffmeister 1956, Lange 1960) and are known to depredate bird nests (Burt and Grossenheider 1976, Hart 1992). Other potential mammalian nest predators, including mice, Abert's squirrels, bobcats, domestic dogs, and rock squirrels were present within our study area (documented by track plates and visual observations by field personnel) but were not recorded depredating nests by video cameras (perhaps because some of these species occur at low densities; C. Kirkpatrick, pers. obs.).

Additional video camera monitoring may be necessary to ascertain whether some of these mammals (especially mice; Bradley and Marzluff 2003, King and DeGraaf 2006) are occasional nest predators within our study system. Some nest predators may avoid or be attracted to nests with video cameras and the track plates provide a means by which one can identify nest predators present in the study system that were not captured by video surveillance. Data from track plates do not provide an unbiased estimate of density or movement rates of nest predators because they are baited and some predators may avoid or be attracted to them, but they do provide information on the suite of potential nest predators and their relative levels of activity (relative to other locations where track plates are placed with similar methods).

The prevalence of mammalian nest predators in our study system is surprising given that snakes are considered to be the principal nest predator of many New World passerine birds (Weatherhead and Blouin-Demers 2004), especially in the southern USA (Thompson 2007). We believe we did not record snakes as nest predators because our study area was: (1) >2,300 m above sea level in an environment thermally inhospitable to most snake species (M. J. Goode, University of Arizona, pers. comm.); and (2) beyond the northern range limits of several montane rattlesnake species (Stebbins 1985), one of which (twin-spotted rattlesnake [*Crotalus pricei*]) is known to occasionally depredate Yellow-eyed Junco nests at high elevation (2,560 m; Gumbart and Sullivan 1990). We observed only two snakes (Sonoran mountain kingsnake [*Lampropeltis pyromelana*] and Arizona black rattlesnake [*Crotalus cerberus*]) near our study plots and none within the boundaries of our study plots despite thousands of person hours in the field from 2002 to 2009 (C. Kirkpatrick, unpubl. data).

Our study is one of the first to use video cameras at real nests to identify nest predators and measure their relative importance in montane forest ecosystems (similar results were obtained in montane forests of northern Arizona where mammals caused 62% of diurnal nest depredations; T. E. Martin, University of Montana, pers. comm.). Additional research is needed to ascertain if mammals are the principal nest predators in other high-elevation environments. Selection

should favor adaptations by birds to reduce exposure to numerous olfactory-oriented, nocturnal nest predators (e.g., gray foxes, woodrats, mice) in montane environments, just as selection is thought to favor behaviors that reduce exposure to visually-oriented, diurnal predators in other ecosystems (Weatherhead and Blouin-Demers 2004). Identifying the commonalities in the suite of primary nest predators within different ecosystems may help explain differences in behavior and life history traits among species of birds. Montane forests in the Santa Catalina Mountains provide an ideal environment to examine these issues given that breeding populations of ground-nesting birds at higher elevations (>2,300 m) are contiguous with breeding populations at lower-elevations (>1,800 m) where snakes and other nest predators are likely to be more common.

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Feeding a Foreign Chick: a Case of a Mixed Brood of Two Tit Species

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ABSTRACT.—We report on a mixed brood of Great (*Parus major*) and Varied (*Poecile varius*) tits. The brood consisted of one Great Tit and five Varied Tits. Incubation and food provisioning to nestlings were by adult Varied Tits, but not by adult Great Tits. The foreign Great Tit nestling tended to receive more food than the average Varied Tit nestling. Provisioning of the foreign Great Tit by Varied Tits lasted even after fledging. We discuss the causes and outcomes of this rare phenomenon. *Received 5 December 2009. Accepted 9 March 2010.*

Nestlings of different species are rarely present in the same nest (Shy 1982), apart from cuckoo-host interactions (Payne 1977, Rothstein 1990). Mixed broods have been reported among several species of passerines including titmice, nuthatches, flycatchers, and thrushes (e.g., Mackenzie 1950, 1954; Slagsvold 1998; Dolenec 2002; Robinson et al. 2005; Govoni et al. 2009). Two types of mixed brood rearing are known: only one species raises foreign young along with their own (Slagsvold 1998), and both pairs from different species raise the mixed brood together (i.e., nest sharing; Robinson et al. 2005, Govoni et al. 2009). The major cause of mixed broods in both cases has been explained as interspecific competition for a desirable nest site.

The occurrence of mixed broods provides an opportunity to investigate the evolutionary origin of interspecific brood parasitism (Slagsvold 1998), and to examine the role of learning in species recognition (Hansen et al. 2008, 2009). However, detailed observations of mixed broods have not been reported with the exception of studies in which researchers experimentally cross-foster eggs between different species (e.g., Slagsvold 1998). This seems to be due to the rarity of occurrence of mixed broods as well as insufficient opportunity for video recordings in past decades.

We report a case of a naturally-occurring mixed brood of two tit species. The mixed brood consisted of one Great Tit (*Parus major*) and five Varied Tits (*Poecile varius*). The Varied Tit pair raised the foreign Great Tit with their own nestlings in the same nest box. Feeding events inside the nest box were video recorded.

OBSERVATIONS

We placed 25 nest boxes (17 × 17 × 30 cm, 3 cm entrance) in a mixed deciduous-coniferous forest in 2006 in Karuizawa, Nagano, Japan (36° 21′ N, 138° 35–36′ E) and monitored them during the breeding season. The forest consisted mainly of Japanese larch (*Larix leptolepis*), Mongolian oak (*Quercus mongolica*), and giant dogwood (*Swida controversa*). Nine of the 25 boxes were used by Great Tits, one box by Varied Tits, and one contained a mixed brood of Great and Varied tits.

We visited the mixed brood nest 11 times in the period of 1 month (5 times during the egg stage, 5 times during the nestling stage, and once on the day of fledging). Incubation by one of the Varied Tit adults (probably the female) was confirmed during the nest visitations, but not by either of the Great Tits. We identified six eggs in the nest and all eggs hatched synchronously on 16 May. The Varied Tit also sat on the naked chicks on the day of hatching. We recorded feeding events inside the nest box during the nestling period by placing a KPC-EX500 CCD camera (KT&C Co., Seoul, Korea) on the ceiling of the nest box connected to a GR-DF590 digital video camera (Victor Co., Kanagawa, Japan). Only the adult Varied Tits provisioned food (caterpillars, bees or spiders) for the nestlings for the entire 805 min recorded, and no adult Great Tits visited the nest box.

We analyzed the provisioning behavior of the adult Varied Tits using the video recordings from inside the nest box. We could easily discriminate between the foreign Great Tit and Varied Tit chicks by morphology in the late nestling stage,

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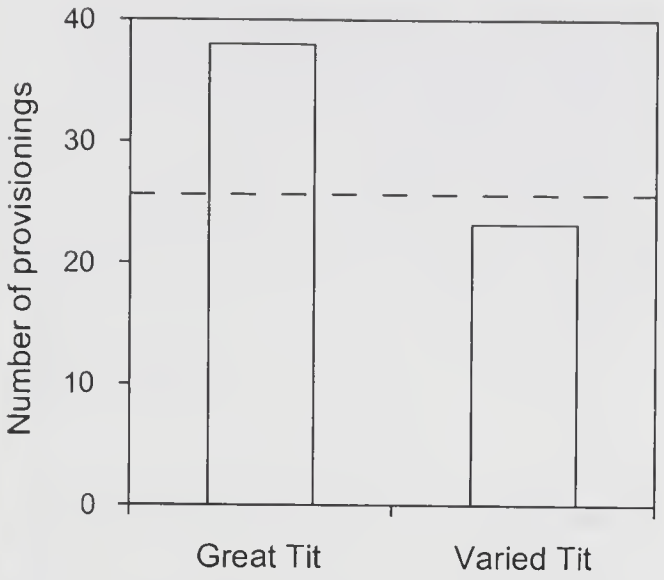

FIG. 1. Provisionings by adult Varied Tits to a foreign Great Tit nestling and Varied Tit nestlings in 480 min of video records. The bar representing the Varied Tit nestlings indicates the mean value for the five nestlings. The broken line indicates the expected number of provisionings if all nestlings are provided with food randomly.

and used the video data recorded at this stage (14, 15, and 16 days of age) for analysis. We analyzed 154 provisioning events during 480 min of video recordings. The adult Varied Tits fed several different nestlings at each provisioning visit ($\bar{x} \pm$ SD: 2.2 ± 0.7 nestlings; ranging from 1 to 4). The mean rate of provisioning visits was 8.8/hr.

We tested whether food provisionings by adult Varied Tits were biased between the Great Tit nestling and the Varied Tit nestlings using a *G*-test (Sokal and Rohlf 1995). A significant difference was found (*G*-test with Williams' correction: $G_1 = 6.36$, $P = 0.012$; Fig. 1) when comparing the observed number of provisionings received by the Great Tit nestling and the five Varied Tit nestlings with the expected number of provisionings (i.e., the value if all nestlings obtain food randomly). This implies the adult Varied Tits provided more food to the Great Tit young than they did to young Varied Tits on average.

All young fledged sequentially between sunrise and noon on 1 June when they were 17 days of age. The Great Tit and Varied Tit fledglings were confirmed to be fed by the adult Varied Tits after fledging.

DISCUSSION

This is the first report of an occurrence of a Great and Varied tit mixed brood, and the first video analysis of a naturally occurring mixed brood. The foreign Great Tit nestling appeared to be smaller than Varied Tit chicks, but it tended to obtain more food than the average Varied Tit nestling (Fig. 1). This appears to be the result of active begging behavior by the Great Tit; it begged for food in 100% of the provisioning visits by the adults, whereas Varied Tit young begged only in 85% of the provisioning visits, on average. The Varied Tit adults fed the Great Tit even after fledging, suggesting they learned to recognize the foreign chick as if it was their own.

This observed mixed brood is unlikely to be due to a new breeding strategy of Great Tits in this population because this is the only known case in our 4-year study (breeding seasons from 2006 to 2009), during which time we monitored 106 nest boxes of cavity-nesting birds. A previous report suggests that Great Tits have not evolved intraspecific brood parasitism (Kempenaers et al. 1995). It is more likely the mixed brood is a nonadaptive by-product of interspecific nest-site competition. Interspecific nest usurpations in our study site were often observed between Great Tits and Varied Tits during the beginning of the breeding season. It may be possible the observed mixed brood occurred either when Varied Tits took over the Great Tits' nest in which one egg had already been laid, or when Great Tits failed to usurp the nest of Varied Tits.

Feeding of a foreign chick is obviously costly for adult Varied Tits, but the fitness consequence for the foreign Great Tit remains unclear. The Great Tit nestling tended to obtain more food than the average Varied Tit nestling, but we cannot reject the possibility that quality and quantity of food may be insufficient for the foreign Great Tit. A previous report suggests the dietary needs of nestlings may be different between these two tit species (Mizutani and Hijii 2002). The Great Tit may also have other costs, such as problems with species recognition when subsequently trying to mate and breed. Species recognition is imprinted early in life, and may be irreversible once it has been established (Hansen et al. 2008, 2009).

The occurrence of mixed broods may represent an initial step in evolution of interspecific brood parasitism (Slagsvold and Hansen 2001). The present observation provides an example that a foreign chick can be raised to fledging by a different species. Future field observations may reveal further examples, which may give us valuable insights into the evolution of interspecific brood parasitism.

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Infanticide by an Eastern Phoebe

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ABSTRACT.—We videotaped an Eastern Phoebe (*Sayornis phoebe*) nest in central Kentucky on 22 June 2008 and documented a case of infanticide. An adult male phoebe, likely the resident male, was captured at the nest site on 21 June 2008. The resident female fed nestlings (3, ~8 days of age) 69 times during a 4.1-hr taping session (0815–1221 hrs EDT) the next day, but the resident male was not observed at the nest. Beginning at 0923 hrs, an intruding phoebe (likely a male) occasionally visited the nest, sometimes pecking at, but not feeding, the nestlings; this phoebe initiated a vigorous attack at 1151 hrs, pecking and pulling the head of one of the nestlings for 25 min before pulling it out of the nest. The intruding phoebe returned after a short absence, just before the end of the videotape, and began attacking another nestling. The nest was empty when checked the next day. Suitable territories and nest sites may be limiting factors for Eastern Phoebes, and infanticide by non-breeding males may enhance their reproductive success if the resident female or a new female subsequently pairs with the male and initiates a new nest. *Received 11 January 2010. Accepted 24 March 2010.*

Infanticide has been reported in many species of birds, primarily in cooperative breeders, colonial breeders, and polygamous species (Freed 1986). Infanticide has been reported among socially monogamous species of birds, but primarily species where breeding opportunities may be limited by biased sex ratios or availability of needed resources such as nest sites (Freed 1986; Robertson and Stutchbury 1988; Møller 1988, 2004). Infanticide may be adaptive either by providing access to a needed resource, such as a nest site (Robertson and Stutchbury 1988), or by shortening the time until a new breeding attempt (Freed 1986).

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Most reports of infanticide among socially monogamous species have involved secondary cavity-nesting species where availability of nest sites may limit breeding opportunities (Freed 1986, Robertson and Stutchbury 1988, Kermott et al. 1991). We report a case of infanticide by an Eastern Phoebe (*Sayornis phoebe*), a non-cavity-nesting species with specific nest-site requirements that may limit breeding opportunities of some individuals.

OBSERVATIONS

We studied Eastern Phoebes at the Blue Grass Army Depot (BGAD) from mid-March to mid-July 2008. The BGAD is in Madison County, Kentucky and encompasses 5,907 ha of pastures with trees and woodlands interspersed throughout. Concrete shelters (about 2.5 × 5 × 2.5 m; n = 54), each with two open doors (1 × 2 m) at opposite corners occur throughout the depot to provide depot personnel with protection in case of emergencies. The shelters are rarely visited by Army personnel, but phoebes readily enter the shelters to nest.

We located a phoebe nest on 21 June 2008 with three nestlings ~8 days of age in a shelter that, for security reasons, we visited infrequently. An adult phoebe entering the shelter was captured in a mist net on the same day and banded with a USGS aluminum band and a unique combination of three colored-plastic bands. The phoebe was identified as a male based on the presence of a cloacal protuberance. Standard measurements were taken and the male, in apparently good condition, was released.

The nest was videotaped from 0815 to 1221 hrs EDT on 22 June 2008 with a camcorder placed 2 m from the nest. The camcorder was protected from the elements in the shelter so we did not retrieve the videotape until the next day (23 Jun 2008). We subsequently reviewed the tape and noted all visits to the nest by adult phoebes as well as any other recorded behaviors or vocalizations.

An unbanded Eastern Phoebe, apparently the resident female, provisioned nestlings at a rate of 16.8 visits/hr during the 4.1-hr videotape; the phoebe banded the previous day (assumed to be the resident male) was not observed at the nest. The female phoebe visited the nest and provisioned nestlings 35 times from 0815 to 1015 hrs, and always exhibited the same behavior, landing at the edge of the nest and quickly feeding a nestling. Another phoebe, also unbanded, but behaving differently, was first observed at 0923 hrs. Over the next 42 min, this phoebe hovered near the nest twice, briefly landed on the edge of the nest three times, and pecked the head of a nestling during two of those nest visits.

During the third hour of taping (1015–1115 hrs), the resident female fed nestlings 16 times; the other phoebe entered the shelter and perched on the camcorder four times, but did not visit the nest. The resident female continued provisioning nestlings during the fourth hour of taping (1115–1215 hrs). The 'intruding' phoebe entered the shelter and perched on the camcorder 21 times from 1115 to 1145 hrs, uttering 'bipeaked vocalizations' (Smith 1969) on multiple occasions and 'initial peaked vocalizations' (Smith 1969) twice. The female visited the nest three times while the other phoebe was on the camcorder; the presence of the intruding phoebe had no apparent effect on the female's behavior.

The intruding phoebe flew to the nest at 1151 hrs and began vigorously pecking and pulling one of the nestlings, focusing its attack on the nestling's head. This phoebe pecked or pulled at the nestling about 1,250 times (~50 times/min) over the next 25 min. The resident female came to the nest ~5 sec after the attack was initiated, hovered briefly at the edge, then landed with beak agape and moved to within ~2 cm of the attacker for ~3 sec. The female then flew from the nest, returning 5 sec later and again briefly hovered near the nest. As the attack continued, the female left and re-entered the shelter and perched on the camcorder three times (but uttered no calls), and flew to the nest and provisioned nestlings five times, uttering no vocalizations and not interacting with the attacking phoebe. The intruding phoebe pulled the apparently dead nestling out of the nest at the conclusion of the 25-min attack, and returned to the nest ~4.5 min later and began attacking a second nestling. The videotape ended 40 sec after this second attack began.

The nest was empty when visited the next day with no sign of adult or nestling phoebes in the shelter. We re-visited the shelter 12 days later; the nest was still empty and we observed no adult phoebes in or near the shelter.

DISCUSSION

Male Eastern Phoebes typically provision nestlings and defend nest sites and territories from conspecifics (Weeks 1994). Thus, the

absence of the male at our focal nest plus the presence of the intruding phoebe suggests the resident male was not present. The male we banded at the nest site, likely the resident male, appeared to be in good condition when released. The reason for the male's absence is unknown, but could have been due either to abandonment of the territory (e.g., as a result of being captured in a mist net) or predation.

Our observations indicate adult Eastern Phoebes at times engage in infanticide. Beheler et al. (2003:996) also noted instances of infanticide ('probably by nonparental adults') by Eastern Phoebes, and Weeks (1994) reported that infanticide at times occurred after a territorial male phoebe disappeared. Phoebes are sexually monomorphic and both males and females utter 'bipeaked' and 'initial peaked' vocalizations (Smith 1969). Thus, we cannot be certain the intruding phoebe in our study was a male. However, the absence of the resident male suggests the infanticidal phoebe was a male. Infanticide by male phoebes may enhance reproductive success if the resident female or a new female subsequently pairs with the infanticidal male and initiates another nest. This behavior has been reported in other species of songbirds, including House Wrens (*Troglodytes aedon*; Freed 1986, Kermott et al. 1991), Tree Swallows (*Tachycineta bicolor*; Robertson and Stutchbury 1988), and Barn Swallows (*Hirundo rustica*; Møller 2004).

Suitable territories and nest sites may be limiting factors for Eastern Phoebes, and competition for these resources may be intense (Beheler et al. 2003). Phoebes occupy a variety of woodland and edge habitats (Graber et al. 1974), but the availability of suitable nest sites may be limited in many areas (Weeks 1994). Thus, some adult phoebes may be non-breeding floaters. Supporting this assumption is the rapid replacement of dead mates and rapid settlement of territories when new nest sites become available (Beheler et al. 2003). The disappearance of a territorial male represents an opportunity for non-breeding males to acquire the resources needed for reproduction. Phoebes are typically double-brooded (Weeks 1994) and, in our study area, second broods are generally initiated in late May or early June; new nests are rarely initiated after late June (GR, pers. obs.). A male phoebe acquiring a territory with 8-day-old nestlings on 22 or 23 June, as in our study, would likely have no opportunity to breed during the current breeding season if those nestlings developed normally and fledged (generally when 16–18 days of age; Weeks 1994). Infanticide could potentially provide a male phoebe with a breeding opportunity. However, the nest in our study was empty when checked 12 days later and we observed no phoebes in or near the shelter, indicating the infanticidal male phoebe in our study did not subsequently breed in that shelter.

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We thank the U.S. Army for allowing us to conduct research at their facility, the EKU Research Committee for financial support, and C. E. Braun, H. P. Weeks Jr., and an anonymous reviewer for helpful comments. A short video clip of the infanticidal phoebe attacking and removing the nestling is posted at http://www.youtube.com/watch?v=4mVQMpyqlrs.

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The Wilson Journal of Ornithology 122(3):623–624, 2010

Marsh Wren Eats Small Fish

Andrea J. Ayers[1,2] and James W. Armacost Jr.[1]

ABSTRACT.—We report an observation of a Marsh Wren (*Cistothorus palustris*) eating a small fish. On 29 November 2008, a Marsh Wren was observed catching and consuming a small fish, probably a mosquitofish (*Gambusia affinis*), in a coastal marsh in Jefferson County, Texas. Marsh Wrens are known to eat invertebrates, primarily insects and spiders, and we believe this is the first record of a Marsh Wren capturing and consuming vertebrate prey. *Received 24 August 2009. Accepted 22 January 2010.*

The Marsh Wren (*Cistothorus palustris*) is a small passerine that inhabits a variety of coastal and interior marshland habitats. Prior observations of the feeding habits of Marsh Wrens indicate they feed strictly on invertebrates, foraging in dense patches of shrubs or along the base of cattail (*Typha* spp.) stalks or other marsh vegetation, on or near the ground or water surface (Bent 1948, Kroodsma and Verner 1997). Marsh Wrens typically move constantly as they forage, gleaning prey from plant surfaces or from on or just below the water surface. Most prey items are too small for a person to identify from a few meters (Kroodsma and Verner 1997). While conducting fieldwork as part of a project to assess avian mortality and population-level effects associated with a transmission line in coastal marshes at the J.D. Murphree Wildlife Management Area (WMA) in Jefferson County, Texas, AJA made an opportunistic observation of a foraging Marsh Wren that captured and consumed a small fish. After reviewing Bent (1948) and Kroodsma and Verner (1997), we believe this is the first report of a Marsh Wren taking live vertebrate prey.

OBSERVATIONS

The J.D. Murphree WMA contains a diverse community of coastal wetlands, including freshwater, intermediate, brackish, and saline wetlands (Texas Parks and Wildlife Department 2008). On 29 November 2008, at ~1000 hrs CST, AJA observed a Marsh Wren perched above a roadside ditch that drained water from a former construction site for the transmission line. A section of the ditch was partially overhung by matted vegetation that was residue from Hurricane Ike, which made landfall on the southeast Texas coast on 13 September 2008.

The Marsh Wren was perched on a small dead limb ~20 cm above and diagonally crossing the running water, looking downstream. The wren sat perched over the water observing small fish swimming below for a short time. While still perched, the wren bent down and plucked a fish from the water, never leaving its perch. The wren captured and handled the fish adeptly, positioning the fish in its beak to swallow it head-first. The wren proceeded to swallow the fish in small increments, alive and whole. We estimated the size of this fish to be approximately twice the length of the Marsh Wren's beak. The exposed culmen of an adult Marsh Wren ranges in size from 12 to 14 mm (Ridgway 1904); thus, we estimate the fish to have been 24–28 mm in length. Afterwards the bird flew from the roadside ditch into denser marsh vegetation. This observation was made from a distance of ~4 m, using 8 × 40 binoculars, and the prey item, which had a silver, reflective body and a noticeable tail fin, was easily identifiable as a fish rather than an invertebrate. We speculate the fish was a mosquitofish (*Gambusia affinis*), based on the type of marshland habitat.

DISCUSSION

This observation occurred 11 weeks after Hurricane Ike made landfall on the southeast Texas coast. The J.D. Murphree WMA was covered by a storm surge that peaked at >4 m and persisted for several days (Berg 2009). This salt water intrusion killed many plants in Texas coastal marshes, and abundance of aquatic invertebrates may have been reduced. A possible explanation for this Marsh Wren's behavior may have been the lack of invertebrate prey, leading it

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to capture and consume a small vertebrate. Marsh Wrens typically forage in dense vegetation, making their foraging behavior difficult to observe (Kroodsma and Verner 1997), and it is possible that vertebrates are a regular, but previously undocumented, component of their diet.

We believe our observation of a Marsh Wren feeding on a small fish is the first record of this behavior and contributes new knowledge about the ecology of this species. Picman et al. (1993) observed Marsh Wrens to destroy eggs and nestlings of competing birds in deep-marsh habitats, while Bump (1986) reported Marsh Wrens appeared to have sampled the contents in four of five cases when they punctured eggs. However, we consider consumption of egg contents incidental, and not primarily a foraging behavior. Larger species of wrens are known to take vertebrate prey on occasion. For example, Cactus Wrens (*Campylorhynchus brunneicapillus*) have been known to feed on amphibians and reptiles (Storer 1920, Proudfoot et al. 2000). It isn't surprising that Marsh Wrens, which feed mainly on aquatic invertebrates (Bent 1948, Kroodsma and Verner 1997), would capture and consume small fish, given that other species of wrens are known to take vertebrate prey on occasion.

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Occasional Mimicry and Night-time Singing by the Western Curve-billed Thrasher (*Toxostoma curvirostre palmeri*)

R. Roy Johnson[1,2] and Lois T. Haight[1]

ABSTRACT.—The first instance of vocal mimicry is reported for the western subspecies of Curve-billed Thrasher (*Toxostoma curvirostre palmeri*). A Curve-billed Thrasher engaged in countersinging with a migrating Black-headed Grosbeak (*Pheucticus melanocephalus*) near Tucson, Arizona. Night-time singing by Curve-billed Thrasher is also documented for the first time. At least three responding Curve-billed Thrashers engaged in spontaneous song near Tucson, Arizona. Additional night-time singing was elicited by playback recordings *Received 13 February 2010. Accepted 24 April 2010.*

The Curve-billed Thrasher (*Toxostoma curvirostre*) is placed in the Mimidae, a family that includes several species that mimic other species and/or sing at night (Bent 1948). Perhaps most widely known is the ability of Northern Mockingbird (*Mimus polyglottos*) to mimic other species, and also sing both day and night during the breeding season (Derrickson and Breitwisch 1992). Mimicry has been reported for the nominate subspecies group of the Curve-billed Thrasher in Texas (Rylander 1981, Tweit 1996), but neither vocal mimicry nor night-time song has been previously documented for the western subspecies (*T. c. palmeri*; Bent 1948, Tweit 1996). The only reference found for possible night-time singing by *T. curvirostre* was by Oberholser (1974: 654), "it seldom sings at night," also referenced by Tweit (1996) but with no specific documentation or reference to source by either publication.

OBSERVATIONS

The western Curved-billed Thrasher has a varied and melodious repertoire, but mimicry of another species was recorded only recently. A Curved-billed Thrasher mimicked a migrant Black-headed Grosbeak (*Pheucticus melanocephalus*) on a desert plot ~23 km east of Tucson, Arizona. The Black-headed Grosbeak was singing near the top of a large ornamental eucalyptus (*Eucalyptus* spp.) tree on 23 April 2009 at ~0830 hrs MST. Another apparent Black-headed Grosbeak was answering from a patch of Sonoran Desert scrub ~35 m away. Singing during spring migration is not unusual for Black-headed Grosbeak but countersinging by the species in desert lowlands is unusual. The grosbeak singing in the eucalyptus tree behaved in typical fashion, commonly giving one or more *chuck* notes between songs, but the bird in desertscrub was not interspersing songs with *chuck* notes. On closer examination with binoculars, the second bird was observed to be a Curve-billed Thrasher near the top of a foothill palo verde (*Parkinsonia microphylla*) tree singing a song that was audibly indistinguishable from that of the grosbeak.

T. c. palmeri has sung both spontaneously and elicited night-time song on this same desert plot. A Curve-billed Thrasher began spontaneous song on 21 February 2005 at 2212 hrs (sunset 1815 hrs). It sang two refrains of several notes, the refrains separated by ~15 sec. The thrasher at site A was answered by a short song from a second thrasher ~150 m distance (site B). Thrasher A sang another short song and was answered by a third thrasher (site C) ~150 m in a different direction at 2213 hrs. Thrashers singing at sites A, B, and C roughly formed an equilateral triangle with spacing of ~150 m between thrashers. This approximates the spacing between *T. curvirostre* males engaged in diurnal territorial song in this area during the breeding season.

The moon was bright on the night of 21 February (full moon 24 Feb) but an ~5 min shower had earlier produced a trace of rain at ~2145 hrs. A thrasher at site A again sang spontaneously on the following night, 22 February, and was answered by a thrasher at site B between 2127 and 2128 hrs. The sky was similar to the previous night with scattered clouds but the moon was bright and visible most of the time.

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DISCUSSION

Diurnal song at this time of year is common for this early nesting species for which breeding readiness peaks in early February (Vleck 1993, Tweit 1996). The Curved-billed Thrasher was not among the 53 listed avian species known to respond to playback tapes by 1980 (Johnson et al. 1981). After not hearing spontaneous singing during the nights following 22 February, a Curved-billed Thrasher song tape was played (Colver et al. 1999) on 27 February. Following five playings of the tape, beginning at 2229 hrs with hesitation between each, a thrasher at site A responded. It sang a refrain of ~six notes at 2233 hrs. A similar song again came from site A at 2234 hrs. after playing the tape two more times. Despite further playing of the tape there was no additional response. A similar response from a thrasher at site A resulted when a tape was played on 28 February, beginning at 2325 hrs. Answers of a half-dozen notes were sung again at 2328 hrs and at 2329 hrs. No further attempts were made to elicit songs.

Neither behavior discussed here has been recorded previously for this species. Because of its close relationship to other mimids that exhibit mimicry and/or nocturnal song, it would be of phylogenetic and general ornithological interest to devise a project, using playback tapes, to further investigate these phenomenon among the subspecies of *T. curvirostre*.

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Ornithological Literature

Robert B. Payne, Review Editor

HANDBOOK OF THE BIRDS OF THE WORLD. Volume 14. Bush shrikes to Old World sparrows. Edited by J. del Hoyo, A. Elliott, and D. Christie, 2009. Lynx Edicions, Barcelona, Spain. 2009: 893 pages, 51 color plates, many photographs and maps. ISBN: 978-84-96553-50-7. 212 Euros (~$310.00 US) (cloth).—The volume continues the series on birds of the world with general accounts on all families and species of birds. This volume includes the Malaconotidae (bushshrikes), Prionopidae (helmetshrikes), Vangidae (vangas), Dicruridae (drongos), Callaeidae (New Zealand wattlebirds), Notiomystidae (Stitchbird), Grallinidae (mudlarks), Struthideidae (formerly Corcoracidae, Australian mudnesters), Artamidae (woodswallows), Cracticidae (butcherbirds), Pityriaseidae (Bristlehead), Ptilonorhynchidae (bowerbirds), Paradisaeidae (birds-of-paradise), Corvidae (crows), Buphagidae (oxpeckers), Sturnidae (starlings), and Passeridae (Old World sparrows).

The text includes a summary of recent molecular studies on systematic relationships, descriptions of each species and subspecies, their behavior and ecology, a list of references, and an index to the common and scientific names. The text was written by ornithologists who have conducted fieldwork on these birds and are familiar with them. All species are well illustrated in the color plates and many are shown in great supporting photographs. The family accounts describe and compare the highlights of the species accounts, which include taxonomy, subspecies and distribution including a map, habitat, food and feeding, breeding, movements, survival, status and conservation concern, and a bibliography. The length of the species accounts varies with what is known about the birds and with the style of the authors.

The Madagascar vangas are amazingly diverse in morphology and most species are not well known. Biological information on these endangered birds might help in conservation plans; but the continuing loss of habitat in Madagascar, even in sites with nominal protection, is the main challenge to their survival.

Cooperative breeding is widespread in butcherbirds, woodswallows, and Australian mudnesters, and the text describes the Rowleys' previously unpublished study of Australian Magpie (*Gymnorhina tibicen*). Courtship displays of bowerbirds and birds-of-paradise are well described and illustrated in photographs. The extreme display structures and decorations of bowerbirds include the maze-like four-walled bower of Yellow-breasted Bowerbird (*Chlamydera lauterbachi*) and the ornamental feathers of King-of-Saxony Bird-of-Paradise (*Pteridophora alberti*) in the bower of Archbold's Bowerbird (*Archboldia papuensis*). Bowerbird young remain in the nest for 17–21 days, except Archbold's Bowerbird which live in cold and wet high-altitude habitats and remain nestlings for 30 days. The 42 species of birds-of-paradise are fascinating in their sexual dimorphism and elaborate displays. None has become extinct since 1600, but three are globally threatened and others are declining in numbers in the wild, especially due to hunting. Conservation efforts have had success in protecting certain populations from hunting and habitat loss. Captive-breeding programs now are feasible and are recommended while the wild populations are still healthy.

The crows are the most species-rich group in Volume 14 with 24 genera, 123 species, and 359 taxa. The section on this family could stand alone as a readable book. Corvids have more than their share of cooperatively-breeding species; the best known is Florida Scrub-Jay (*Aphelocoma coerulecens*). Some corvids have a complex layer of social organization with the pair, the family group, and the flock (Red-billed Chough [*Pyrrhocorax pyrrhocorax*]). Resident singles or pairs of Common Raven (*Corvus corax*) chase single intruders from carcasses but, when the intruders recruit other vagrants to join them, the group can overcome the aggressiveness of the resident territorial birds. Ravens, American Crow (*C. brachyrhynchos*), and Rook (*C. frugilegus*) each have more than 20 distinct calls of known function. The geographic variation in calls of Large-billed Crow (*C. macrorhynchos*) requires further study. Some corvids including the Common Raven are good vocal mimics of other species in captivity and others are mimics in the

wild (Eurasian Jay [*Garrulus glandarius*]); the function of mimicry in wild corvids remains a mystery. Common Ravens associate with gray wolf (*Canis lupus*) in Yellowstone National Park, USA and the scavenging corvids get early access to the carcass at wolf kills. Food-storing and retrieval is common in several corvids; one, Clark's Nutcracker (*Nucifraga columbiana*), buries pine (*Pinus* spp.) seeds in places that lose their snow cover at different times in spring allowing nutcrackers to have a steady supply of seeds through a season. Some crows are common and widespread, but the Hawaiian Crow (*Corvus hawaiiensis*) is now extinct in the wild; new birds from a captive breeding group may be reintroduced in the future, although birds reared and released in the 1990s soon died from predation and disease.

Starlings have a wide range of breeding organizations, some are cooperative breeders, some are densely colonial, and some are polygynous, all much like the unrelated New World blackbirds (Icteridae). Some Passeridae sparrows (here treated as 40 species), are highly colonial, as up to 20 nests of Spanish Sparrow (*Passer hispaniolensis*) have been built in a single nest of White Stork (*Ciconia ciconia*), and colonies of this sparrow have as many as 800,000 pairs.

This volume includes a Foreword that discusses the influence of bird watchers on the interest in and concern for birds. "Birding past, present and future—a global view" compares the roles of great men and social change in times past, advances in field guides and the web as information resources, advances in optics, cameras, and recording devices, and the availability of local and overseas tours to see birds. The demographics and economic impact of birders have been surveyed mainly in the U.S. and U.K. In the U.S., 20 million people consider themselves birders, getting into the field at least 50 times a year. The economics of birding may amount to US$31.7 billion, counting vehicles, fuel, guides, food and lodging including ecotours, plus $1.9 billion on optics and $2.6 billion on nest boxes, feeders and bird food. Birds benefit from birders in projects for conservation, and a concern for responsible ecotourism includes training local guides and support of birding places. Birding is promoted as exciting and intellectually challenging, and a passion for the natural world that is thought to benefit our physical and emotional health and wellbeing.

The volumes of the *Handbook of the Birds of the World* are written clearly and well illustrated, and they are the highest standard source of information on birds. When Volume 16 is published in late 2011, the series will be the first work to describe in words and illustrations all species of birds in the world.—ROBERT B. PAYNE, Professor Emeritus, University of Michigan, 1306 Granger Avenue, Ann Arbor, MI 48104, USA; e-mail: rbpayne@umich.edu

GROUSE OF PLAINS AND MOUNTAINS: THE SOUTH DAKOTA STORY. By Lester D. Flake, John W. Connelly, Thomas R. Kirschenmann and Andrew J. Lindbloom. South Dakota Department of Game, Fish and Parks, Pierre, South Dakota, USA. 2010: xv + 246 pages, and ~173 color photographs and 27 graphs. ISBN: 9780615350158. $15.00 (Soft cover).—This lavishly illustrated book with color photographs and graphs is intended for the general public but is prepared to also appeal to biologists, scientists, managers, and anyone interested in grouse in the prairies of North America. The authors are well known for their interest in grouse and several have impressive research and teaching credentials. This is a book about four species of grouse native to South Dakota: Sharp-tailed Grouse (*Tympanuchus phasianellus*), Greater Prairie-Chicken (*T. cupido*), Greater Sage-Grouse (*Centrocercus urophasianus*), and Ruffed Grouse (*Bonasa umbellus*). The latter is the least expected as one does not associate aspen (*Populus* spp.) forests with the grasslands and shrublands of the Great Plains. Greater Sage-Grouse have the smallest distribution at present in South Dakota followed by Ruffed Grouse, Greater Prairie-Chicken, and Sharp-tailed Grouse with the most extensive range across the state. All four species are hunted with modest (sage-grouse) to expansive seasons (the other 3 species).

This book is based on science and accumulated field experience. It has 13 chapters, six appendices, and an extensive Literature Cited. The presentation is pleasant and easily understood but the information is supported by citation of the scientific literature. The chapters are: South Dakota's Grouse Species, Physical Characteristics, Behavior, Mobility and Habitat, Nutritional Needs and Food Habits, Nesting Ecology, Broods, Survival and Mortality, Population Monitoring, Hunting Seasons, Grouse Hunting, Habitat Loss,

and Further Thoughts. Each chapter is heavily illustrated (only color photographs and graphs are used), covers each of the species, and ends with a Review (= summary).

Each chapter is interesting and well prepared and there is something for everyone. I was interested in all of the material but especially the material (pages 3–4) on Dusky Grouse (*Dendragapus obscurus*), which may have been present historically, although poorly conducted transplants failed to establish a population after releases in 1969 and 1974. Greater Sage-Grouse are at the extreme eastern edge of their current (only 3 counties in South Dakota) and historical range in South Dakota. One wonders how this species survives in areas with low densities of big sagebrush (*Artemisia tridentata* subspp.). Silver sagebrush (*A. cana*) obviously will support sage-grouse; the presence of robust, taller grasses with more cover is likely important in supporting sage-grouse at the eastern and northern peripheries of their distribution. Ruffed Grouse are also an anomaly as they appear to have low dispersal capability but somehow found their way to the isolated Black Hills (most likely from the west). Management of public lands (USDA, Forest Service) in the Black Hills for ponderosa pine (*Pinus ponderosa*) does not benefit Ruffed Grouse, which has more affinity for species of aspen and other deciduous shrubs. Relatively little is known about Ruffed Grouse in South Dakota, which the authors acknowledge but try to fill the data gaps with published information from scientific studies in other states.

The authors are candid about the role of hunting and are cautious about possible population effects (with literature citations) on grouse. There are two chapters (10 and 11) that discuss data that can be obtained from hunter-harvested birds, as well as the joy of being afield with hunting dogs in the fall. They describe how data are collected (Chapter 9) and provide actual data on counts in spring as well as harvest estimates. They are quick to note the inadequacies of some surveys but do not discuss how state wildlife agencies place priorities on how funds are spent (obviously on species where hunter interest is high and where grouse populations are large). The photographs amply demonstrate that grouse also have value for bird watchers, especially in spring during breeding seasons.

Scattered throughout the text and focused in the final chapter (13), the authors discuss some of the habitat issues involved with grouse populations. These include everything from West Nile virus (pond development for livestock and energy production which may enhance mosquito distribution) to livestock grazing, federal land conservation programs, prairie and forest management, fences and roads to wind turbine farms. These issues are not restricted to South Dakota but occur throughout the Great Plains and the Intermountain West.

I was hard pressed to find factual errors and any editorial glitches, but did find Dalke italicized on page 61, and a missing parenthesis on page 73. Use of jargon such as 'input' is relatively minor throughout. With rare exceptions (i.e., page 208, hectares and acres), the authors do not use metric terms and we read about pounds and inches and miles. Several references in the Literature Cited (T. D. I. Beck and J. L. Beck, M. M. McDonald and J. E. McDonald) are not alphabetical. A nicer problem is that there may be too many similar photographs. One weakness is there is no Index.

The stated goal of this book (Foreword) is "to foster increased interest and appreciation for South Dakota's four grouse species and the habitats that support them." The book clearly meets this goal as it is very attractive, the material is accurate and current, it is well written and easy to read, and the color photographs keep inviting you to turn the next page. This book is a must for everyone interested in grouse and the northern Great Plains, and I highly recommend it.—CLAIT E. BRAUN, Grouse Inc., 5572 North Ventana Vista Road, Tucson, AZ 85750, USA; e-mail: sg-wtp@juno.com

FARMLAND BIRDS ACROSS THE WORLD. Edited by Wouter van der Weijden, Paul Terwan, and Adriaan Guldemond. Lynx Edicions, Barcelona, Spain. 2010: 144 pages and 500 + color photographs, maps, and figures. ISBN: 13-978-84-96553-63-7. $39.00 (hardcover).—Books that aim to highlight conservation issues can sometimes be downers that bring to mind Aldo Leopold's famous quote: "Being an ecologist is living in a world of wounds." Others can tend to act as generally unfriendly encyclopedias of information, useful only to conservation planners. *Farmland Birds Across the World* is a unique creation. It highlights the importance of agricultural habitats to global birdlife in a way that is accessible, informative, and engaging to the casual reader, ecologist, and conservationist alike.

It does so using more than 500 stunning large format photographs of birds and the agricultural landscapes they inhabit that invite the reader on a journey around the globe. It is authored by seven experts in biology and links the beauty and natural history of birdlife to the challenging and often complex conservation issues facing birds in agricultural landscapes. One unique way they convey these stories is by peppering the chapters with separate boxed-off panels highlighting specific conservation issues (e.g., declines in Asian vultures due to veterinary drugs), conservation-related natural history stories (e.g., the journey of the Black-tailed Godwit [*Limosa limosa*]) and interesting on-the-ground conservation efforts (e.g., novel planting schemes that benefit skylarks). This makes the book easy to pick up, even for just a moment.

The introduction is a short overview that highlights the complex, mutual relationships between farming and birds that can be both beneficial and negative. It highlights interesting paradoxes. For example, agriculture and its intensification represent perhaps the most important threat to bird populations globally, yet agricultural lands also represent the sole remaining habitat for many critically endangered species. Chapter 2 effectively begins the body of this book and represents an overview of issues related to farming such as factors affecting birds in crops, resources that crops can provide to birds, the ecosystem services provided by birds to crops, crop damage by birds, and how farming can adversely impact birds.

The next six chapters focus on birdlife in specific agricultural environments: grasslands, cereal and other annual crops, rice fields, orchards and plantations, coffee and cacao, and farmyards. The first page of each chapter contains a global map of the distribution of each agricultural crop and some brief statistics impressively illustrating the global nature and extent of agriculture. For example, cereals are the world's most important calorific crop, occupying approximately one-third of all arable land. The authors highlight how changes in the area and cultivation intensity of crops, the birdlife exploiting these crops, and the threats to bird populations vary by region. Notably, they draw on massive global bird and agricultural data bases to create figures illustrating the worldwide trends in human activity shaping bird populations.

Each chapter ends with another unique feature, a bulleted section outlining different conservation challenges and opportunities associated with issues like global climate change, agricultural policy, farming practices and, at times, a surprising and conspicuous lack of information. For example, the authors (page 67) mention, "Although China is the world's leading rice producer, little is known on birdlife in its rice fields than the occurrence of herons and egrets."

The final chapter discusses the future prospects for farmland birds, summarizing some of the grand conservation challenges and highlighting interesting and unique solutions to those problems. Collectively, this volume manages to convey the authors' excitement at the richness of farmland birdlife, their confusion due to the paradoxes associated with bird conservation and agricultural production, their fear at the often overwhelming threats facing farmland bird populations, and finally relief there are potential solutions to improve the fortunes of farmland birds.

My only significant complaint about this volume was the limited treatment given to the potential importance of biofuel production on avian biodiversity. The authors do give significant mention of the widespread impacts that oil-palm (*Elaeis* spp.) is having on tropical birds. However, second generation cellulosic biomass crops that may include cereals, trees and woody plants, and other crops have potential to radically reshape agricultural landscapes worldwide. To be fair, little is known about the ecological effects of many of these crops, but I felt the threat of biofuels to farmland birds should have made lists of conservation threats.

It is estimated that over one-third of the earth's surface has now been converted to agricultural uses. This makes the book a particularly timely resource. A notable asset of this volume is that it does a seamless job of integrating scientific ideas into the chapters in a way that is accessible to non-scientists. It is this feature that makes the book so broadly appealing, yet useful even to conservation scientists. Biologists often think of themselves as storytellers and the authors of *Farmland Birds Across the World* have succeeded in telling fascinating and important stories that instill a sense of global responsibility for the birds that are impacted by the growing of our food, fiber, and fuel.—BRUCE A. ROBERTSON, Research Associate, Great Lakes Bioenergy Research Center, Kellogg Biological Station, Michigan State University, 3700 East Gull

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BIRDS OF EUROPE, SECOND EDITION. By Lars Svensson. Princeton Field Guides, Princeton University Press, Princeton, New Jersey, USA. 2009: 448 pages, 3,500+ color illustrations. Illustrations and captions by Killian Mullarney and Dan Zetterström. ISBN: 978-0-691-14392-7. $29.95 (paperback).—The text covers all 772 species of birds occurring in Europe as well as 32 introduced species or variants and 118 vagrant species. In the United Kingdom, where it was published by Harper/Collins, it is known as the "*Collins Bird Guide*." The book is a substantial revision of the author's first edition (1999). The book includes all bird species that breed or regularly occur in Europe, Africa north of 30° N, the Sinai Peninsula, the Middle East through Turkey, Israel, Jordan, Syria, Georgia, and Azerbaijan, and the Canary Islands and Madeira. Europe is bordered on the east by the Ural Mountains, Ural River, and Caspian Sea.

The text and distribution maps are on one page and the illustrations are on the facing page. For each species the text has a description of shapes, male and female, young and old, breeding and nonbreeding, and geographic variation where appropriate. The text is clear, concise, and accessible, and generally more detailed and comprehensive than in North American field guides. For example, in one of the longer species accounts, the description of Rough-legged Hawk/Rough-legged Buzzard (*Buteo lagopus*) has 441 words, each well chosen. Key identification features are highlighted in italics, variations in plumage within a population are shown and described, and differences between similar species are noted; e.g., the wing pattern in flight is helpful in identification of larks. Habitat, range, and breeding status are described with notes on frequent hybridization. Many species have useful descriptions of feeding behavior and breeding biology. The Middle Spotted Woodpecker (*Dendrocopos medius*), unlike other related woodpeckers, calls but does not drum in territorial assertion. Voice is described in words, often with cadence- and pitch-perfect transliteration: the species-typical call of Rock Ptarmigan (*Lagopus muta*) is "here comes the bride". Species status (breeding, resident/migratory, abundance) is noted in short form for Britain and Ireland. Each family has an informative account with comments such as the night vision of owls is not "surreal" but requires light from the moon or stars. Other useful sections are included on seawatching (and how to point out birds on a featureless seascape to other watchers), raptors in flight, and general advice for identification of waders/shorebirds and gulls.

The quality of the illustrations is very good, the birds lifelike, the details precise, the selection comprehensive. Many birds are illustrated in more than one posture and in flight. The color plates include in small type many useful comments on identification. Because more than one standard taxonomic source is currently used in ornithology, the species recognized in the book reasonably follow "author's preference" in recent revisions. For example, in the Herring Gull (*Larus argentatus*) species complex, where 2½ pages of color plates have 67 images, several species are recognized that previously were known as subspecies; these are American Herring Gull (*L. smithsonianus*), Yellow-legged Gull (*L. michahellis*), Armenian Gull (*L. armenicus*), Audoin's Gull (*L. audouinii*), and Caspian Gull (*L. cachinnans*). Some distinctive forms recognized as subspecies receive detailed accounts as well; e.g., "Steppe Buzzard" (*Buteo buteo vulpinus*). The owls are particularly well illustrated with new images for this edition, and the comments on these birds ("stately look", "deceptively gentle look", "grim look", "astonished look", "austere look") capture the impression so the reader can identify the live owl in the field. Wallcreeper (*Tichodroma muraria*) is described as "The Hoopoe [*Upupa epops*] of the rock face!" Hawfinch (*Coccothraustes coccothraustes*) has a big head; "the Hawfinch is a flying pair of nutcrackers!" A few plumages are shown that do not appear in North American field guides, e.g., summer plumage of female Long-tailed Duck (*Clangula hyemalis*), and some comparisons of North American species go beyond what is said in North American field guides, e.g., adult Buff-breasted Sandpiper (*Tryngites subruficollis*) adults are similar to (and distinguishable from) juvenile Ruff (*Philomachus pugnax*). Most North American *Catharus* thrushes are illustrated with spotted juvenile wing coverts, perhaps the appropriate plumage if most vagrants that appear in Europe are birds in their first autumn, but the text should indicate the age in these birds, as it does for first-winter New World warblers. Two pages on the

pochards (*Aythya* spp.) show hybrids and the most similar non-hybrids with notes for identification.

Vagrant species are illustrated along with similar resident or breeding species, or are in the back of the book, and accidentals are listed but not described. Introduced species are in the main section of the book (e.g., Canada Goose [*Branta canadensis*]) or in the back of the book (e.g., the estrildid finches with established populations).

The book is an excellent field guide, small enough to use in the field, a clear and informative read on birds, and clearly the best book for identification of the birds of Europe. It also will be useful in North America especially in identification of northern Palearctic vagrants in Alaska and elsewhere. It is highly recommended.—ROBERT B. PAYNE, Professor Emeritus, University of Michigan, 1306 Granger Avenue, Ann Arbor, MI 48104, USA; e-mail: rbpayne@umich.edu

CONSERVATION BIOLOGY OF HAWAIIAN FOREST BIRDS. Edited by Thane K. Pratt, Carter T. Atkinson, Paul C. Banko, James D. Jacobi, and Bethany L. Woodworth. Yale University Press, New Haven, Connecticut, USA. 2009: 707 pages, 97 black and white plus 32 color illustrations. ISBN: 978-0-300-14108-5. $85.00 (cloth).—Hawaiian forest birds are famous among evolutionary biologists for their spectacular bill morphology and bright plumage. They are equally famous among conservation biologists for extinction, declines, and numerous threats. This book touches on the former but focuses on the latter. It appears to largely summarize the USGS, Biological Research Discipline efforts from a recent grant. This may explain why they ignore much other research on Hawaiian birds.

The book is organized into five parts. Part 1 is introductory and has three chapters that deal with origins, historic decline and extinction, and forest birds and Hawaiian culture. Part 2 on status, biology, and limiting factors has 11 chapters on monitoring, trends, habitat loss and degradation, food exploitation, life history and demography, malaria and pox virus, genetics, mammalian predators, Hawaiian raptors, introduced birds, and epidemiology of malaria and pox. Part 3 is about applying research to management, including controlling invasive species, landscape ecology, managing disease, controlling small mammals, and captive propagation. Part 4 deals with recovery programs for four species, one of which is likely extinct, a second is close behind, a third is rapidly declining even though it has been extensively studied for more than 20 years, and the fourth is a success story. Part 5 deals with the future, and covers the social and political obstacles and asks the question "Can Hawaiian forest birds be saved?" Space limits chapters in the book that can be reviewed.

The origins and evolution chapter by Thane Pratt is masterful historical biogeography, both in understanding where Hawaiian birds came from as well as initial conditions they likely encountered. We understand why these are the main vertebrates of Hawaiian forests, and a non-random set of potential colonists. They competed among themselves, which led to adaptive radiation, but did not compete with amphibians, reptiles, mammals, or social insects.

There are two excellent chapters on disease. One deals with modeling the epidemiology of avian malaria and pox; the other concerns managing disease. The former is a particularly clear exposition of compartmentalized modeling for understanding transmission dynamics in a vector-transmitted disease such as malaria. The chapter on managing disease considers diverse techniques for controlling mosquitoes and pigs (*Sus scrofa*) to break transmission, along with immunizing the birds themselves and genetically modifying mosquitoes. Unfortunately, these chapters, as well as the one on genetics and conservation, ignored our prize-winning and widely cited 2005 paper (Condor 107: 753–764) documenting an increase in avian malaria in highest elevation forest where pigs were managed. This is a clear example that mosquitoes documented in the forest may have originated from unmanaged lands, a point emphasized by the book.

No specific adaptations were identified in the book, despite intensive studies that have been performed by several research groups. Banko and Banko, in their chapter on evolution and ecology of food exploitation, deal with comparative bill morphology as adaptation for particular diets, but they ignore work documenting that the Iiwi (*Vestiaria coccinea*) has undergone a niche shift with accompanying changes in bill morphology. Woodworth and Pratt, in their chapter on life history and demography, ignore nestling overgrowth and seasonal variation in sex allocation in the Hawaii Akepa (*Loxops coccineus coccineus*),

clear adaptations for breeding during a seasonal decline in food. These have been dismantled by competition with introduced Japanese White-eyes (*Zosterops japonicus*), documented in Evolutionary Ecology Research 10: 931–965 (2008) (= EER 2008), referenced and dismissed in the book.

The Banko and Banko chapter on food essentially ignored arthropod prey in *Metrosideros polymorpha* trees for insectivorous birds. This is the most important tree in wet to mesic Hawaiian forests, and EER 2008 shows that most birds use foraging substrates associated with the tree. They refer to an old dissertation, not the papers that document the diversity of prey with seasonal pattern of variation. A reader might think that *Scotorythra* caterpillers are the most important food resource for all bird species. Like other islands, Hawaii has a preponderance of spiders.

The chapters in the book on monitoring forest birds and identifying trends are thorough but misleading. The authors fail to recognize analysis of residuals as essential when modeling changes in populations over time. A regression model requires residual analysis to ensure the model fits the data. If it does not, the model needs to be corrected. The trends reported for Hakalau Forest National Wildlife Refuge are incorrect, as shown in our paper in the May 2010 issue of Condor (112: 213–221), because their residuals indicate significant lack of fit. The endangered Hawaii Akepa and the Iiwi, a species of concern, are significantly declining on the refuge. An example in the book that clearly indicates the lack of fit is Fig. 25.6 in the chapter on saving Hawaiian birds. The endangered Hawaii Creeeper (*Oreomystis mana*) has a 21-year trend that looks positive, but residuals are negative in the early and late years of the series, and positive in the middle, indicating lack of fit. The creeper is declining, not increasing, in models with an additional parameter with appropriate residuals.

The chapter by Jeff Foster on introduced birds provides a marvelous historical and ecological perspective. Unfortunately, he dismisses EER 2008 because of the trend analysis. He argues that food limitation can only be established by measuring food. However, ornithologists have long recognized that food limitation can be inferred by stunted growth of nestlings, fault bars in wing and tail feathers that reflect nutritional stress during molt, lower fat, and changes in begging patterns.

Woodworth and Pratt in the life history and demography chapter have a section on human-caused changes in demographic rates, but only report on nesting success. We (EER 2008), document significant change in juvenile survival and adult survival in the Hawaii Akepa associated with increase in numbers of introduced Japanese White-eyes. Chewing lice (Phthiraptera) are not even mentioned in the book although they contribute to parasite-mediated competition.

Most chapters in this book have to be read critically, because they ignore important literature and accept misleading trend analysis. The answer to "Can Hawaiian forest birds be saved?" is "No" unless the immediate threat is recognized and managed. That threat is an introduced bird, which has stunted growth and lowered survival throughout the community (2009. Current Biology 19: 1736–1740). Malaria will kill remaining birds that are food limited because they will be unable to mount energetically expensive immune responses.—LEONARD A. FREED, Department of Zoology, University of Hawai'i, Honolulu, HI 96822, USA; e-mail: lfreed@hawaii.edu

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COVER: Wilson's Plover (*Charadrius wilsonia*). Illustration by Don Radovich.

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FRONTISPIECE. Henslow's Sparrows (*Ammodramus henslowii*) are tallgrass prairie specialists in North America. Analysis of yearly resettlement and abundance patterns from Breeding Bird Survey data indicated this species is less likely to return to previously used breeding areas than other grassland sparrows. Restricting analyses to single observer-collected data resulted in significant effects not detected in data aggregated from multiple observers during the same study period. Acrylic painting by Marco Antonio Pineda M of Puebla, Mexico.

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BREEDING PATTERNS OF HENSLOW'S SPARROW AND SYMPATRIC GRASSLAND SPARROW SPECIES

L. LYNNETTE DORNAK[1]

ABSTRACT.—Henslow's Sparrows (*Ammodramus henslowii*) are reported to have irregular patterns of return to breeding areas. I present data supporting these reports at rangewide extents, while testing potential biases inherent in the North American Breeding Bird Survey data. Two measures of population variability were used to show that Henslow's Sparrows are less likely to use breeding areas predictably and consistently, but have similar variance in numbers at occupied sites relative to other sympatric grassland sparrow species. I illustrate how restricting analyses to single-observer-collected Breeding Bird Survey data results in subtle but significant effects not detected in data aggregated from multiple observers through the study period. The most conservative analysis (single-observer, restricted distribution) showed that Henslow's Sparrows exhibited lower prevalence of occurrence than Grasshopper (*Ammodramus savannarum*) ($P < 0.001$) and Savannah (*Passerculus sandwichensis*) ($P < 0.001$) sparrows but no difference in variation of abundance ($P > 0.05$). These results suggest Henslow's Sparrows are not returning to previously used breeding habitat from year-to-year. Grassland management should consider the behavior documented in this study and attempt to incorporate this facet of Henslow's Sparrow biology into decisions that involve broad-scale landscape design. *Received 27 January 2010. Accepted 8 May 2010.*

Artificial grazing regimes, drainage of wetlands, large-scale agriculture, and alteration of natural fire regimes have changed North American landscapes, and left behind only relict tracts of native prairie (Hyde 1939; Knopf 1988, 1994). The full extent of these impacts on native flora and fauna has only recently begun to be appreciated. Shifts are likely occurring continent-wide, but the most dramatically impacted habitat has been native grasslands. Since European settlement, 99.9% of native prairies have been lost (Samson and Knopf 1994) or altered (Vickery et al. 1994) in North America, and they are now termed a critically endangered habitat (Noss et al. 1995). Thirteen bird species within this biome have incurred serious declines, far surpassing those of any other North American biome (Knopf 1994, Peterjohn and Sauer 1999, Robbins et al. 2002, Powell 2006), probably the result of continued conversion of prairie habitat to an artificial landscape.

Henslow's (*Ammodramus henslowii*), Grasshopper (*A. savannarum*), and Savannah (*Passerculus sandwichensis*) sparrows are obligate grassland nesters (Vickery et al. 1994) with population declines across part or all of their breeding ranges (Peterjohn and Sauer 1999, Wells and Rosenberg 1999). None has national threatened or endangered species status, but Henslow's and Grasshopper sparrows have been listed as Birds of Conservation Concern (USDI 2008) and Species of Continental Importance (Rich et al. 2004). However, the species' behavior and habitat use, as it relates to landscape configuration, must be

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understood more fully before successful management can be achieved.

Hyde (1939:23) was the first to note the unpredictability of Henslow's Sparrows appearance in breeding areas, writing "its presence in a given season cannot be certainly predicted," a sentiment that has been repeated by other authors (Wiens 1969, Skipper 1998, Ingold et al. 2009). Most studies report low (Skipper 1998, Monroe and Ritchison 2005) or nonexistent site fidelity for Henslow's Sparrows in breeding areas (J. L. Zimmerman cited in Pruitt 1996). This behavior is atypical compared to Grasshopper and Savannah sparrows which exhibit higher nest site fidelity (Bédard and LaPointe 1984, Wheelright and Rising 1993). These studies have used site fidelity as a measure of return rates to breeding areas in consecutive years, and have necessarily concentrated at only a few sites. Thus, a broader-scale assessment of annual resettlement patterns in breeding areas is necessary, but is lacking in the literature.

Henslow's Sparrows may be also erratic and opportunistic in selection of sites for breeding on a broad spatial scale. Previous research on this species has focused at local and regional scales with a few exceptions (e.g., Herkert 2007). The only studies that used landscape-level analysis were limited to sections of the species' range (Bajema and Lima 2001, Cunningham and Johnson 2006, Thogmartin et al. 2006), and little information exists to provide a range-wide perspective for this species.

I examined abundance data from the entire breeding range for Henslow's Sparrows, and compared it to similar data for Grasshopper and Savannah sparrows. The focus was not to compare habitats used by each species; instead, I analyzed patterns of resettlement in habitat the birds already had assessed as suitable for nesting. Grasshopper and Savannah sparrows were chosen for comparison, not because of similarity or dissimilarity of habitat choices, but because they are obligate grassland species that nest within the breeding range of Henslow's Sparrow. I used North American Breeding Bird Survey (BBS) data (Sauer et al. 2007) to address two objectives. First, I examined how Henslow's Sparrow populations vary in time and space. A secondary objective was to assess the impact of using different subsets of BBS data because these data have been criticized for inherent biases. This information is critical to understanding this species' natural history, as well as conservation implications that may be derived.

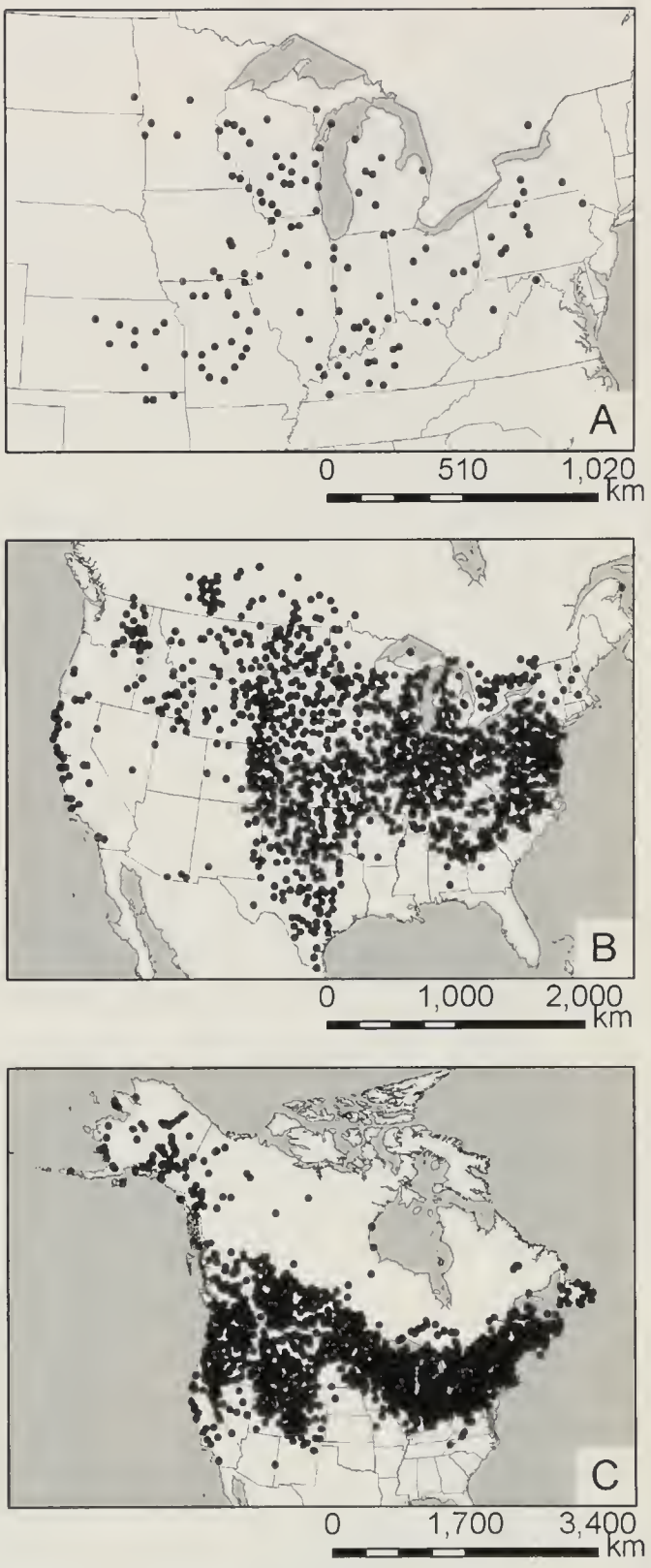

FIG. 1. Henslow's (A), Grasshopper (B), and Savannah (C) sparrow distributions from Breeding Bird Survey route data collected during 2000–2007. Henslow's, Grasshopper, and Savannah sparrows were observed on 132; 1,387; and 1,765 routes, respectively.

METHODS

Study Area.—The study area included the entire breeding ranges of Henslow's, Grasshopper, and Savannah sparrows (Fig. 1). All bird abundance data were derived from the BBS, a monitoring

system created in the 1960s with the goal of understanding long-term trends in North American breeding bird populations (Sauer et al. 2007). BBS data are collected annually, on fair-weather June mornings, on 4,100 standardized roadside census routes across the United States, Canada and, most recently, Mexico. Sampling points are spaced evenly along the survey route (Robbins et al. 1986), which is 39.4 km in length; 50 sampling points are located every 0.8 km along the route. Observers record all birds seen or heard during 3 min at each stop. Data are available for all years between 1966 and the present, but I used data from 2000–2007 to assure maximal route density and consistency.

Count Data.—I used two measures to describe the magnitude of yearly fluctuations of resettlement across ranges of these species: prevalence of occurrence (proportion of years present) and variation in abundance. The former describes how consistently a species returns to a given BBS route year after year, and is calculated as the ratio of the number of years in which a species was detected on a route to the number of times during the study period the route was surveyed. The latter measures year-to-year variation in number of individuals of a species at the site and is estimated as the coefficient of variation: the standard deviation data divided by the mean abundance for each route across all years in which the route was surveyed. Routes sampled in only 1 year of the study period were excluded from analyses because the coefficient of variation was undefined. These two variables describe the consistency of occurrence and abundance, but saturation effects of variation in abundance may influence my results.

The BBS data were divided and analyzed in four groups to consider potentially inherent biases (geographic and observer). (1) BBS routes were considered across the entire breeding range of each species. (2) Analysis was constrained to BBS routes within the recorded breeding range of Henslow's Sparrows. I also examined BBS route data collected by single observers across all years in the study period, removing possible biases originating from differences in observer consistency. These analyses were conducted (3) across the entire range of each species, and (4) only within the distributional area of Henslow's Sparrow. The smallest data set had 56 routes and, to have equal samples size for each analysis, I randomly selected 50 routes per species for each data set.

Statistical Analysis.—Shapiro-Wilk normality tests and Levene's test for homogeneity of variances were performed on all data sets. At least one sample within each data set had non-normally distributed data and unequal variances. Both negative and positive skews were common within data sets, and transformation of the data was not possible. Thus, I used Kruskal-Wallis nonparametric analysis of variance to test for differences among means, which provided conservative and consistent testing for differences among all groups. Kruskal-Wallis test statistics were evaluated with $\alpha = 0.05$. Mann-Whitney *U*-tests were performed to differentiate between significant groups whenever significant χ^2 values were obtained. I used the non-parametric Kendall's tau statistic to analyze the relationship between prevalence of occurrence and variation in abundance. A Bonferroni correction was applied to Mann-Whitney *U*-tests and Kendall's tau correlations, and all effects were reported at $\alpha = 0.0167$. Statistical analyses were performed using SPSS, Version 16.0 (2007). All maps were created in ArcGIS, Version 9.2 (ESRI 2009).

RESULTS

Prevalence of Occurrence.—Significant differences were found among species in all data sets tested for prevalence of occurrence ($P < 0.001$). There were significant differences between species for the multiple-observer data set, both at the full extent of the species' ranges and within the distribution of Henslow's Sparrows (Table 1). Mann-Whitney *U*-tests for the full extent of the species' ranges indicated the median prevalence of occurrence for Henslow's Sparrows (0.50) was lower than for Grasshopper (0.78, $P = 0.006$), and Savannah (1.00, $P < 0.001$) sparrows; Grasshopper Sparrows, did not differ significantly in prevalence from Savannah Sparrows ($P = 0.022$, Table 2). Results constrained to within the distributional area of Henslow's Sparrow were similar, and significant for all comparisons (Tables 1, 2; Fig. 2).

There were significant among-group differences in the single-observer data sets for both the full-range extent and within the distributional area of Henslow's Sparrow ($P < 0.001$, Table 1). Median Henslow's Sparrow prevalence (0.50) for full-range extents was significantly lower than for Grasshopper (0.88, $P < 0.001$), and Savannah (1.00, $P < 0.001$) sparrows (Table 2). Grasshopper Sparrows had lower prevalence than Savannah

TABLE 1. Comparisons (Kruskal-Wallis tests) of Henslow's, Grasshopper, and Savannah sparrows between multiple- and single-observer groups, and between data collected across the full extent of each species' breeding range versus restricted to Henslow's Sparrow's distributional area. Breeding Bird Survey data were collected from 2000 to 2007 on 50 randomly selected routes. (*) indicates $P \leq 0.05$.

	Full extent of species' ranges						Henslow's Sparrow distributional area					
	Multiple observers			Single observer			Multiple observers			Single observer		
	H	df	*P*	*H*	df	*P*	*H*	df	*P*	*H*	df	*P*
Prevalence of occurrence	26.9	2	<0.001*	39.9	2	<0.001*	45.4	2	<0.001*	45.1	2	<0.001*
Variation in abundance	9.0	2	0.011*	12.6	2	0.002*	2.7	2	0.26	8.1	2	0.018*

Sparrows ($P = 0.005$, Table 2). The same results occurred when these data were restricted to the distributional area of Henslow's Sparrow (Tables 1, 2; Fig. 3).

Variation in Abundance.—Results were less consistent between data sets than for prevalence comparisons. There were differences between species ($P = 0.011$, Table 1) for the multiple-observer data set across the full extent of the species' ranges. Grasshopper Sparrows had higher variability in abundance (median = 0.54) than Henslow's Sparrows (0.42, $P = 0.004$), but no significant differences existed between Henslow's and Savannah (0.50, $P = 0.070$) sparrows, or between Savannah and Grasshopper sparrows ($P = 0.18$, Table 2). No differences were apparent between species (Table 1, Fig. 2) when the data were limited to the distributional area of Henslow's Sparrow.

The single-observer data sets revealed a similar pattern, but with significant differences between species in analysis of the full extent ($P = 0.002$) and within the distribution of Henslow's Sparrow ($P = 0.018$, Table 1). There was no difference between Henslow's Sparrows and Grasshopper (0.44, $P = 0.090$) or Savannah ($P = 0.21$, Table 2) sparrows. Grasshopper Sparrows, however, did (median = 0.47) have higher variability than Savannah Sparrows (0.39, $P < 0.001$). The same results were obtained for analyses limited to single-observer routes within the distribution of Henslow's Sparrow (Tables 1, 2; Fig. 3).

Correlation of Prevalence and Variation.—Prevalence of occurrence was significantly and positively correlated to variation in abundance for Henslow's Sparrows in the multiple-observer ($\tau = 0.37$, $P < 0.001$) and single-observer ($\tau = 0.32$, $P = 0.003$) data sets. This relationship did not hold for either Grasshopper or Savannah sparrows in any data set (all $P > 0.05$).

TABLE 2. Comparisons (Mann-Whitney *U*-tests) of Henslow's (HESP), Grasshopper (GRSP), and Savannah (SASP) sparrows between multiple- and single-observer groups, and between data collected across the full extent of each species' breeding range and restricted to Henslow's Sparrow's distributional area. Breeding Bird Survey data were collected from 2000 to 2007 on 50 randomly selected routes. One comparison for variation in abundance is lacking because of nonsignificant results (Kruskal-Wallis analysis). (*) indicates $P \leq 0.0167$.

	Full extent of species' ranges						Henslow's Sparrow distributional area					
	Multiple observers			Single observer			Multiple observers			Single observer		
	U	*z*	*P*	*U*	*z*	*P*	*U*	*z*	*P*	*U*	*z*	*P*
Prevalence of occurrence												
HESP × GRSP	856.5	−2.7	0.006*	649.5	−4.2	<0.001*	582.0	−4.7	<0.001*	625.5	−4.4	<0.001*
HESP × SASP	505.0	−5.2	<0.001*	422.5	−5.9	<0.001*	364.5	−6.3	<0.001*	347.0	−6.4	<0.001*
GRSP × SASP	938.0	−2.3	0.022	879.0	−2.8	0.005*	998.5	−1.9	0.045	933.5	−2.5	0.014*
Variation in abundance												
HESP × GRSP	830.5	−2.9	0.004*	1,003.5	−1.7	0.09				1,152.5	−0.7	0.50
HESP × SASP	987.5	−1.8	0.070	1,068.0	−1.3	0.21				1,009.0	−1.7	0.10
GRSP × SASP	1,056.5	−1.3	0.18	697.0	−3.8	<0.001*				815.0	−3.0	0.003*

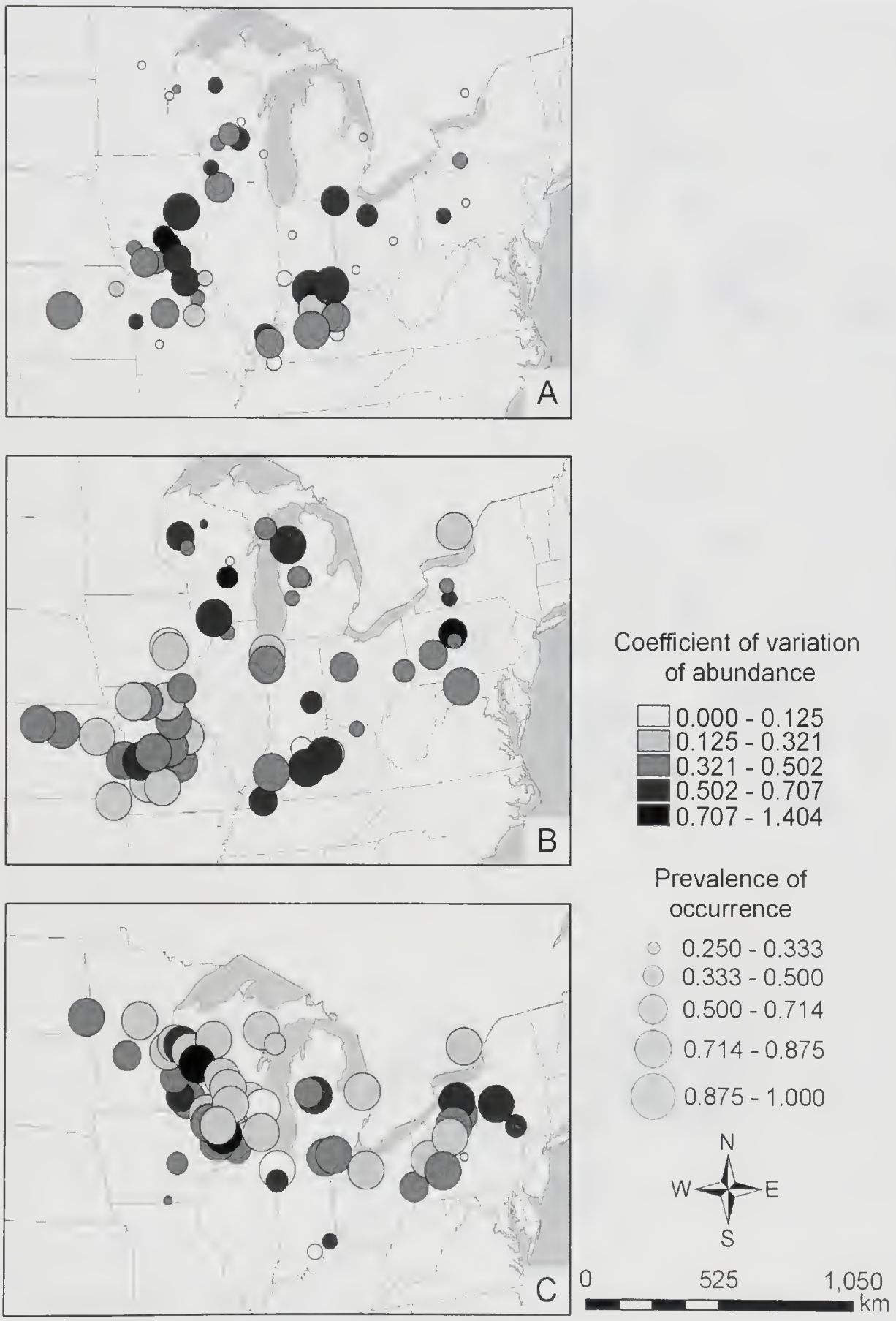

FIG. 2. Henslow's (A), Grasshopper (B), and Savannah (C) sparrow distributions showing prevalence (circle size) and abundance (shading of circles). Data are restricted to within the Henslow's Sparrow's breeding distribution and were collected by multiple observers from 2000 to 2007 on 50 randomly selected Breeding Bird Survey routes.

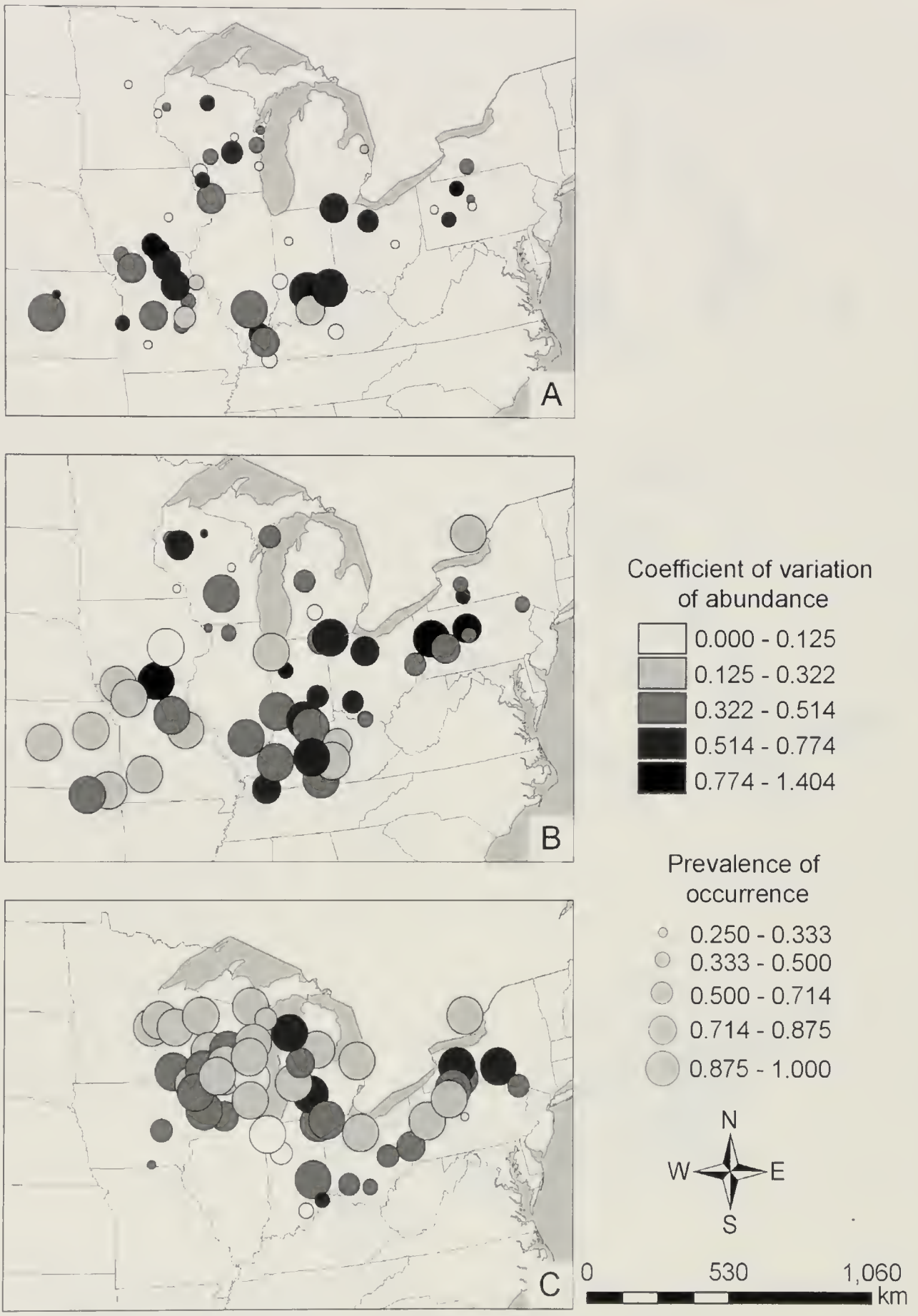

FIG. 3. Henslow's (A), Grasshopper (B), and Savannah (C) sparrow distributions showing prevalence (circle size) and abundance (shading of circles). Data are restricted to within the Henslow's Sparrow's breeding distribution but were collected by single observers only for given routes from 2000 to 2007 on 50 randomly selected Breeding Bird Survey routes.

DISCUSSION

Resettlement.—Site fidelity describes the likelihood of an individual's return to a particular site from year to year. Often, the decision for adult birds to return to a particular site is based on the individual's experiences, or the experiences of conspecifics, at the site in previous years (Hildén 1965). This measurement is ideal for finer-scale analyses, but broad-scale studies require consideration of resettlement of an area by groups of individuals. More importantly, global patterns exhibited by these groups across space and time can provide insight into differences across their geographic ranges.

Previous studies have evaluated nest site fidelity in Henslow's, Grasshopper, and Savannah sparrows (Bédard and La Point 1984, Skipper 1998, Jones et al. 2007), although, to my knowledge, this study is the first to examine variation in resettlement patterns across their breeding ranges. Henslow's Sparrows, in all analyses, had the lowest prevalence of occurrence among the three species. They were, as a group, less likely to return to a BBS route from 1 year to the next. Henslow's Sparrows when detected, with the exception of one test, had variability in abundance not distinguishable from those of Grasshopper and Savannah sparrows. Both Grasshopper and Savannah sparrows had greater numbers of high-prevalence routes than Henslow's Sparrows. These across-species differences in variation in occurrence might be best explained by habitat choices and social behavior of each species.

Henslow's Sparrows require large, open grasslands (Hyde 1939, Smith 1968, Thogmartin et al. 2006). Vegetation structure, including aspects of vegetation height (Wiens 1969, Herkert 1994a) and density (Wiens 1969, Zimmerman 1988), is an important factor for nest site selection by Henslow's Sparrows (Graber 1968, Bajema and Lima 2001, Powell 2006). Fields must remain relatively undisturbed for several consecutive years to achieve vegetation structure typical of Henslow's Sparrow's breeding habitat. Thus, this sparrow avoids fields frequently disturbed by haying (Graber 1968, Cully and Michaels 2000), burning, or grazing on frequent rotations (Bollinger 1995). Similarly, Grasshopper and Savannah sparrows prefer natural habitat to managed landscapes (Owens and Myers 1973, Dale et al. 1997). These species are less strict in their habitat preferences, unlike Henslow's Sparrows, and take advantage of a greater variety of habitats, including grazed, cultivated (Owens and Myers 1973), and hay fields (Graber 1968, Dale et al. 1997).

These differences in habitat preferences among the species may explain differences in prevalence of occurrence. The narrowness of breeding habitat preferences of Henslow's Sparrow within the dynamic grassland biome possibly motivates groups of individuals to seek unused habitat when previously settled locations are no longer suitable (Reinking et al. 2000). For example, an area that is optimal habitat in 1 year may experience a disturbance, such as a late summer burn, resulting in unsuitable habitat for subsequent breeding seasons, thereby encouraging Henslow's Sparrows to seek new nesting locations. Settling suitable habitat when encountered upon arrival in the breeding area, rather than homing to a previously used site and then relocating, would also be advantageous for species that use highly variable resources (Johnson and Grier 1988). Grasshopper and Savannah sparrows use a wider variety of habitats (Smith 1968, Wiens 1969, Owens and Meyers 1973, Dale et al. 1997), and may resettle an area in successive breeding seasons, even though the habitat has been altered from previous years. The ability to be opportunistic and flexible when choosing a nesting location may be advantageous for species whose nesting habitat is unpredictable and patchy (Wiens 1973, Cody 1985, Johnson and Grier 1988).

Henslow's Sparrows, in the relatively few areas where they occurred consistently, had higher variation in abundance. They had less variation in abundance in areas where they were not consistently present creating a positive association between prevalence and variability. This pattern might be explained by the effect of clustering, combined with opportunistic settling. The earliest literature on Henslow's Sparrows noted the tendency of the species to nest in loose colonies, especially when occupying large patches of habitat (Hyde 1939, Graber 1968, Wiens 1969). Individuals of nomadic species, such as Henslow's Sparrows, arriving to an area may use the presence of conspecifics which have already settled there as a means to evaluate habitat quality, especially when knowledge of nest success from previous years within that nesting location is lacking (Bollinger and Gavin 1989, Ahlering et al. 2006). Thus, clustering when paired with opportunistic location selection may

produce a pattern of irregularity of settlement with regularity of abundanee. Unlike Henslow's Sparrows, no significant relationship exists between variability, prevalenee, and abundanee for either Grasshopper or Savannah sparrows.

Biases in BBS Data.—Use of BBS data is a timely and eost-effeetive way of answering relatively short-term, broad-seale questions (Sauer et al. 2005, Winter et al. 2006). The BBS is the only source for range-wide, standardized data in North Ameriea; it is eommonly used to estimate abundanees and year-to-year fluetuations aeross speeies' breeding ranges (Bibby et al. 2000, Diefenbach et al. 2003, Herkert 2007). Although widely used, the BBS is not without potential bias. One critieism of the BBS is that of ehange of observers aeross time. Link and Sauer (1998) suggested that differenees in ability among observers may influenee trends deteeted along routes over time. I found results differed when data were limited to single-observer routes. Speeifieally, Savannah Sparrows had signifieantly higher prevalenee rates than Grasshopper Sparrows in the single-observer data set, a differenee not detected in analyses of the multiple-observer data set. The differenee was signifieant in both the full extent of the speeies' ranges and in the area; thus, redueed to the distributional area of Henslow's Sparrow, the effeet was not a result of geographie extent. Removing routes surveyed by multiple observers also affeeted variation in abundance. There were eontrasting differenees between species aeross the full extents of the speeies' ranges. Grasshopper Sparrows had the highest variability, but the ranks of the other two speeies shifted. The multiple-observer data set in analyses constrained to within the distribution of Henslow's Sparrow showed no speeies differenees, but the single-observer data set revealed signifieant differences.

Thus, results of several analyses ehanged when route data eolleeted by multiple observers were removed. This variation is likely a result of ehange in observers and their relative abilities (Link and Sauer 1998). Sauer et al. (1994) suggested abundanee patterns are best represented by analyses of single-observer data only. However, even single observers may, through time, improve in identification and detection skills, for example by learning a song (Link and Sauer 1998) or the opposite (e.g., with declining hearing abilities); these effeets cannot be measured, but may be redueed by comparisons with multiple-observer data.

Detection.—Other concerns not addressed within the analyses of this paper should be considered. It is possible that Henslow's Sparrows are not detected as easily as Grasshopper or Savannah sparrows. The speeies may be too rare in some areas, resulting in deteetion diffieulties (Wells and Rosenberg 1999, DeVault et al. 2002). In other loeations where individuals are more abundant, lack of aetivity (Diefenbaeh et al. 2007, Confer et al. 2008), or failure to detect individuals may eause discrepaneies, thereby affecting eount data.

Henslow's Sparrow's eryptie appearanee and seeretive behavior (Hyde 1939), in addition to its insect-like song (Leftwich and Ritehison 2000), may lead to deteetion problems during surveys. Deteetion may be further restrieted when singing deelines after mate pairing (Leftwieh and Ritehison 2000) or as a result of Henslow's Sparrows' proelivity for nocturnal singing (Walk et al. 2000). Henslow's Sparrows may not nest near roadsides as a response to woody vegetation (Patten et al. 2006) or traffie volume (Forman et al. 2002), yet BBS data are eolleeted entirely from roadside routes. It is possible that populations of birds are not surveyed aeeurately beeause of species' behavior and surveying teehniques. Bajema et al. (2001) suggest applying a eorrection factor to estimate Henslow's Sparrow abundanee to eounter these deteetion problems.

CONSERVATION IMPLICATIONS

Henslow's Sparrow was onee thought to be prevalent throughout the western extent of its breeding range, although it now oeeupies less than 1% of this original area (Robbins et al. 2002). Its need for regular, although infrequent, habitat disturbanee to maintain a partieular seral stage may faeilitate this decline in present human-dominated landseapes (Pruitt 1996). This habitat in the pre-European landseape was maintained by fire (natural and artifieial), and grazing by large herbivores, ereating a mosaie of habitats on the landseape (Knopf 1994, Umbanhowar 1996). Burning, grazing, and mowing have all been recommended as suitable management practices (Pruitt 1996), but the timing, extent, and frequeney of these disturbanees are critieal faetors that affeet suitability of the habitat for breeding Henslow's Sparrows (Herkert 1994a, Powell 2006). The patterns doeumented in this study are strongly suggestive of a speeies that has adapted to be able to traek optimal sites in a shifting habitat mosaic.

Henslow's Sparrows are also eonsidered area-

sensitive and affected by patch size of breeding habitat (Herkert 1994b, Walk and Warner 1999, Oleary and Nyberg 2000, Thogmartin et al. 2006). The current approach of conserving large isolated patches of high-quality habitat may be too narrowly focused on this concept. Renfrew and Ribic (2008), in a study of Bobolinks (*Dolichonyx oryzivorus*), and Grasshopper and Savannah sparrows, concluded that patch-size might only be particularly restrictive when the entire landscape is heavily fragmented. Thus, conserving smaller areas in addition to large, contiguous habitat patches within the landscape matrix would create more total grassland habitat and better suit Henslow's Sparrows, as it enhances the overall quality of the landscape and fosters its nomadic movements and colonial behavior (Horn and Koford 2006, Ribic et al. 2009). Acquiring smaller, but functional, plots may be easier and more economical, thus producing more immediate conservation impacts. Ultimately, losses of suitable grassland nesting habitat on regional scales may result in extinction of obligate grassland species (Vickery et al. 1994), and particularly Henslow's Sparrows, which appear to move much more broadly across regional landscapes than the other two species analyzed.

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INFLUENCE OF WOODY VEGETATION ON GRASSLAND BIRDS WITHIN RECLAIMED SURFACE MINES

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ABSTRACT.—We examined the influence of woody vegetation on reclaimed surface mines on relative abundance of Grasshopper Sparrows (*Ammodramus savannarum*), Henslow's Sparrows (*A. henslowii*), Eastern Meadowlarks (*Sturnella magna*), Savannah Sparrows (*Passerculus sandwichensis*), Bobolinks (*Dolichonyx oryzivorus*), and Dickcissels (*Spiza americana*) as well as nest-site selection and nesting success of Grasshopper and Henslow's sparrows and Eastern Meadowlarks. Grasshopper and Henslow's sparrows were the most abundant grassland species on reclaimed mines. Numbers of Grasshopper, Henslow's, and Savannah sparrows, and Bobolinks were negatively associated with percent cover of woody vegetation within 100 m of survey locations. Only Grasshopper Sparrows responded to woody vegetation at nest-patch scales, as random locations had >2.5 times as much woody cover as nest locations. Daily nest survival (DNS) was negatively associated with amount of woody vegetation within 100 m of Grasshopper (DNS 0.76 ± 0.001 SE) and Henslow's sparrow nests (DNS 0.94 ± 0.020 SE), but only marginally negatively related to daily nest survival of Eastern Meadowlark nests (DNS 0.87 ± 0.006 SE). Avoidance of woody vegetation by grassland birds and the comparatively lower daily nest survival of Grasshopper and Henslow's sparrow nests near woody vegetation suggests managers of reclaimed surface mines who manage to conserve grassland birds should direct efforts towards reducing woody encroachment. *Received 22 June 2009. Accepted 14 July 2010.*

Grassland birds have declined more rapidly than any other group of birds in the Midwest over the past 30 years (Peterjohn and Sauer 1999, Cully and Michaels 2000, Vickery and Herkert 2001, Sauer et al. 2005). Among the most precipitously declining are area-sensitive species including Grasshopper Sparrow (*Ammodramus savannarum*), Henslow's Sparrow (*A. henslowii*), and Eastern Meadowlark (*Sturnella magna*) (Herkert 1994). These declines have been largely attributed to changes in agricultural practices (Johnson and Igl 2001), habitat loss (Askins 1993), and habitat degradation and fragmentation (Herkert 1994, Cully and Michaels 2000, Vickery and Herkert 2001). Large gains in native and managed grassland habitats in the Midwest are unlikely to occur and successful conservation of grassland birds will require consideration of new opportunities to provide quality grassland habitat for area-sensitive grassland-breeding species. Reclaimed surface mines represent one opportunity to manage for grassland bird species (Whitmore and Hall 1978, Whitmore 1980, Wray et al. 1982, Bajema et al. 2001, DeVault et al. 2002, Monroe and Ritchison 2005, Galligan et al. 2006). Reclaimed surface mines represent a conservation paradox in that grassland birds occupy them even though they are highly disturbed, dominated by exotic grasses, and vulnerable to invasion by exotic woody vegetation such as autumn olive (*Elaeagnus umbellata*).

Woody encroachment is a key management issue with the potential to impact the conservation value of reclaimed surface mines for grassland-breeding birds. Reforestation of mined areas to the original deciduous forest landscape is often not possible due to poor soil conditions (Wray et al. 1982, Brothers 1990, DeVault et al. 2002, Scott et al. 2002), but invasion by woody species such as autumn olive and black locust (*Robinia pseudoacacia*) commonly occurs if left unmanaged (Rummel and Brenner 2003). The decision to maintain open grasslands by removing woody vegetation remains controversial despite known negative effects of woody vegetation on grassland birds (Bajema et al. 2001, Ribic and Sample 2001, Bakker et al. 2002, Fletcher and Koford 2002, Grant et al. 2004). Removal of woody vegetation within reclaimed surface mines may alleviate nest predation by redistributing movements of common mammalian nest predators including common raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and Virginia opossum (*Didelphis virginiana*) (Winter et al. 2000). However, some grassland species such as Vesper (*Pooecetes gramineus*) and Clay-colored (*Spizella pallida*) sparrows, and Common Yellowthroats (*Geothlypis trichas*) may be tolerant of woodland encroachment at the landscape scale (Grant et al. 2004).

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Effective encouragement and conservation of grassland birds on reclaimed surface mines requires an understanding of the influences that unmanaged woody plant encroachment can have on distribution, nest-site selection, and nesting success of obligate grassland birds. We focused on six obligate grassland bird species receiving national and regional conservation attention (Walk and Warner 2000, Bajema et al. 2001, Vickery and Herkert 2001, DeVault et al. 2002): Henslow's Sparrow, Grasshopper Sparrow, Eastern Meadowlark, Savannah Sparrow (*Passerculus sandwichensis*), Bobolink (*Dolichonyx oryzivorus*), and Dickcissel (*Spiza americana*). We examined: (1) how woody vegetation features were related to habitat use and distribution of Grasshopper, Savannah, and Henslow's sparrows, Eastern Meadowlarks, Bobolinks, and Dickcissels breeding within reclaimed surface mines; (2) the extent woody habitat features were related to nest-site selection of Grasshopper and Henslow's sparrows, and Eastern Meadowlarks; and (3) if these woody habitat features affected daily nest survival of Grasshopper and Henslow's sparrows, and Eastern Meadowlarks.

METHODS

Study Area.—This study was conducted on reclaimed surface mines within wildlife management areas in eastern Ohio, USA, managed by the Ohio Department of Natural Resources (ODNR), Division of Wildlife. Collectively, these wildlife management areas represent the range of reclaimed surface mine habitats available to grassland birds in eastern Ohio. Tri-Valley Wildlife Management Area (WMA) in northern Muskingum County is ~6,100 ha comprised of ~50% open land (grasslands, wetlands, and food plots), 40% woodland, and 10% brushland. Approximately 2,600 ha of reclaimed grasslands are within Tri-Valley WMA. Woodbury WMA in southern Coshocton County is ~7,600 ha of ~35% openland (grasslands, wetlands, and food plots), 8% brushland, and 57% woodland. Approximately 1,200 ha of reclaimed grasslands are within Woodbury WMA (ODNR 2007).

Dominant vegetation types in the study area were non-native cool season grasses including fescue (*Festuca* spp.), redtop (*Agrostis gigantea*), timothy (*Phleum pratense*), and orchard grass (*Dactylis glomerata*) as well as native warm season grasses including switchgrass (*Panicum virgatum*), Indian grass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), and little bluestem (*Schizachyrium scoparium*). Native and non-native forbs (*Melilotus* spp., *Trifolium* spp., *Solidago* spp., *Lotus corniculatus*), and woody vegetation including autumn olive, black locust, blackberry (*Rubus allegheniensis*), multiflora rose (*Rosa multiflora*), lespedeza (*Lespedeza* spp.), flowering dogwood (*Cornus florida*), and pines (*Pinus* spp.) were also well represented.

Surveys.—Grassland birds were surveyed from May through July 2005 and 2006 at 101 different point-count locations in Tri-Valley (24 in 2005 and 29 in 2006) and Woodbury (24 in 2005 and 24 in 2006). We used a systematic random sampling design for point-count locations. Starting locations (6 per study site) of point-count survey transects were randomly selected using a Geographic Information System (GIS); subsequent point-count locations were systematically placed 250 m apart until it was not possible to place the next point 250 m from the previous location (i.e., barrier such as a woodland area or large wetland complex). All point-count locations (n = 101) were recorded with a handheld Global Positioning System (GPS) unit. We performed grassland bird surveys at each of the 101 point-count locations three times each from 15 May to 15 July in both 2005 and 2006 between 0630 and 1100 hrs EST on days without fog, precipitation or winds >25 kph. Two trained observers first allowed a 2-min period for birds to adjust to surveyor presence at each point-count location followed by a 6-min survey period when all singing male grassland birds were recorded within a 100 m radius. The time of detection of each bird was recorded during each point-count survey along with species code and straight-line distance (m) to each bird detected with the use of a laser rangefinder (Ransom and Pinchak 2003).

Nest Survival.—We randomly selected eight of 16 5-ha study plots similar in topography within the grassland units containing varying amounts of woody encroachment for nest searches (4 within Woodbury and 4 within Tri-Valley). Field teams used a spot-mapping protocol (Bibby et al. 2000) to identify breeding territories to facilitate locating nests. Grids were visited eight times during morning hours as part of the spot-mapping efforts from 1 May to 16 June 2005 and 2006, and an observer walked the entire 5-ha plot on parallel transects (separated by 75 m). These spot-maps helped field teams extensively search plots for nests of Grasshopper and Henslow's sparrows,

and Eastern Meadowlarks from 1 May to 1 August 2005 and 2006. We initially conducted nest searches using rope-dragging techniques where a 30-m rope was dragged behind two individuals while a third walked several meters behind the rope looking for birds that flushed from nests. We also relied on behavioral cues to find nests and carefully followed adults that were carrying food and nesting material until a nest was located. Observers systematically searched known breeding territories obtained from spot maps to locate nests. Some nests were located by chance during bird surveys and while taking vegetation measurements. We marked nest locations with a handheld GPS unit as well as with one colored flag placed 5 to 10 m from the nest depending on how concealed the nest was to avoid flushing the attending adult. We checked nests every 3–4 days during the incubation period and every 2–3 days when young neared the fledging stage. Nests were visited from different angles during each nest check to avoid creating paths that may attract predators. The number of eggs and/or nestlings, date the nest was checked, and the species name were recorded. A nest was considered active if at least one egg was present. A typical nest period for the three focal species was 26 days with 8–10 days post-hatching to fledge young (Ingold 2002). We considered a nest successful if at least one young fledged or if it was active for ≥8 days post-hatching (Vickery 1996) and there were no obvious signs of predation. A nest was considered lost to predation if the eggs were removed, cold or broken or if the nest was disturbed and the nestlings were no longer in the nest during the first week post hatching (Ingold 2002).

GIS Analysis.—We estimated the amount of woody vegetation within 100 m of nests and survey points using National Agricultural Imagery Program (NAIP) aerial photographs from 2005 and 2006 of Coshocton and Muskingum counties, which were projected using ArcGIS 9.1 (ESRI 2005). The percentage of woody vegetation and number of woody patches were estimated for circular plots with a 100-m radius centered on each nest (n = 81) and on all GPS survey locations (n = 101). We visited plots and directly compared vegetation shown in images to actual vegetation on plots observed during field visits to verify the size of woody plants detectable in aerial photographs. Ground-truthing revealed woody vegetation patches <4 m^2 in area were not reliably detected from aerial photographs; consequently patches of woody vegetation ≥4 m^2 in size were defined as woody vegetation patches. Each woody patch of vegetation ≥4 m^2 within 100 m of each nest and survey point was digitized and the area of each polygon was used to calculate the total area of woody vegetation within a 100-m radius surrounding each nest and survey location. The total percent of woody vegetation was calculated by dividing the total area (m^2) of woody vegetation by the total area of the circle (31,415 m^2) multiplied by 100. Aerial photographs, projected in ArcGIS 9.1, were used to measure the distance (m) from each nest and each survey location to the nearest woodland edge.

Statistical Analyses.—We compared an *a priori* set of woody vegetation variables (percent cover of woody vegetation, number of woody patches, and distance to woodland edge) on bird survey locations to identify which woody vegetation features were used as cues by grassland birds in selecting suitable habitat. We used 101 survey locations as replicates to identify woody habitat features used by Grasshopper, Henslow's, and Savannah sparrows, Eastern Meadowlarks, Bobolinks, and Dickcissels as cues in selecting suitable habitat for breeding locations. The relationship between relative abundance and woody vegetation was tested using regression analysis in Proc GENMOD (SAS Version 9.1; SAS Institute 2002) using generalized linear models. Bird point-count data were transformed when appropriate to minimize non-normality and variance heterogeneity. A log transformation was applied to counts of Grasshopper and Henslow's sparrows, and Eastern Meadowlarks and a normal distribution was used. A Poisson distribution was used for counts of Savannah Sparrows, Bobolinks, and Dickcissels.

Percent woody vegetation, number of woody vegetation patches ≥4 m^2, and the distance from plot center to the nearest woodland edge were moderately correlated (r < |0.5|) and were incorporated into a principal components analysis (Proc FACTOR in SAS Version 9.1; SAS Institute 2002) to characterize woody vegetation surrounding survey locations using a single parameter. The first factor of the three principle components explained >56% of the variation in woody vegetation among survey points (Eigenvalue = 1.69). This first factor loaded positively for percent woody cover (0.88) and number of woody patches (0.70), and loaded negatively for distance to woodland edge (−0.65).

We examined an *a priori* set of woody vegetation variables (percent cover of woody vegetation, number of woody patches, distance to nearest woody patch, and distance to woodland edge) at individual nests and random locations to learn which woody vegetation variables influenced grassland birds during nest-site selection. We used 81 nests as replicates to identify woody habitat features used by individual birds (Grasshopper and Henslow's sparrows, and Eastern Meadowlarks) to select nest-site locations for each species independently during individual nest attempts. We transformed the variables when appropriate to minimize non-normality and variance heterogeneity. Percent woody vegetation, number of woody vegetation patches, and distance from plot center to the nearest woody patch and woodland edge were used in a discriminant function analysis (Quinn and Keough 2002) (DFA; Proc CANDISC in SAS Version 9.1; SAS Institute 2002) to examine which variables best discriminated between nest and random plots. Variables that best discriminated between nest and random plots were interpreted as potential habitat cues used by grassland birds in selecting locations for nest placement (Quinn and Keough 2002).

We examined how woody habitat features in nest plots and at nests influenced nest success by incorporating the first principal component describing woody vegetation surrounding nest sites (PCwood) into the logistic-exposure method (Shaffer 2004) to model daily nest survival rates of Henslow's and Grasshopper sparrows, and Eastern Meadowlarks. This approach models the success or failure of nests during each interval between nest checks and evaluates the probability of nest success over a range of values for influential categorical and continuous explanatory variables. Nest losses to all sources were classified as failures. Nests abandoned prior to laying or found after depredation had already occurred were excluded. We fit the model (PCwood interacting with species) with Proc GENMOD (SAS Version 9.1; SAS Institute 2002) using a binomial response distribution (interval nest fate = 1 if success, and 0 if fail) and provided the user-defined logit link function ($g(\theta) = \log_e (\theta^{1/t}/[1 - \theta^{1/t}])$) where t = the length of the interval (Shaffer 2004).

RESULTS

Grasshopper and Henslow's sparrows were the most abundant species on Tri-Valley and Woodbury WMAs during 2005 and 2006. We detected 1,491 birds on point counts during the study, including 732 Henslow's Sparrows, 465 Grasshopper Sparrows, 209 Eastern Meadowlarks, 39 Bobolinks, 31 Dickcissels, and 15 Savannah Sparrows. Mean relative abundance ranged from 2.33 birds per survey point for Henslow's Sparrows at Tri-Valley to 0 for Savannah Sparrows and Bobolinks at Woodbury. The amount of woody vegetation was negatively associated with abundance of Grasshopper Sparrows (Beta estimate = -0.14 ± 0.041 SE; $\chi^2 = 11.34$, $P \leq 0.001$), Henslow's Sparrows (Beta estimate = -0.15 ± 0.051 SE; $\chi^2 = 7.73$, $P = 0.005$), Savannah Sparrows (Beta estimate = -2.47 ± 0.975 SE; $\chi^2 = 7.38$, $P = 0.007$), and Bobolinks (Beta estimate = -2.35 ± 0.745 SE; $\chi^2 = 11.48$, $P \leq 0.001$), but not significantly for Eastern Meadowlarks (Beta estimate = -0.11 ± 0.241 SE; $\chi^2 = 0.21$, $P = 0.65$) or Dickcissels (Beta estimate = -0.57 ± 0.704 SE; $\chi^2 = 0.84$, $P = 0.36$) (Fig. 1).

Forty-five Grasshopper Sparrow, 18 Henslow's Sparrow, and 18 Eastern Meadowlark nests were monitored during the nesting seasons. Habitat variables discriminated between random locations and nest sites of Grasshopper Sparrows (Canonical correlation = 0.25, Likelihood ratio = 0.936; Wilks' Lambda $F_{3,142} = 3.24$, $P = 0.024$) (Table 1). Random locations had >2.5 times as much woody vegetation as nest locations of Grasshopper Sparrows ($F_{1,144} = 5.41$, $P = 0.021$). Nest placement by Grasshopper Sparrows was not associated with number of woody patches ($F_{1,144} = 1.75$, $P = 0.19$) or distance to woodland edge ($F_{1,44} = 0.96$, $P = 0.33$). Habitat variables did not discriminate between random plot locations and nests of Henslow's Sparrows (Wilks' Lambda $F_{3,114} = 1.12$, $P = 0.35$) or Eastern Meadowlarks (Wilks' Lambda $F_{3,114} = 1.35$, $P = 0.26$) (Table 1).

Twenty of 45 (44%) Grasshopper Sparrow nests, sixteen of 18 (89%) Henslow's Sparrow nests, and nine of 18 (50%) Eastern Meadowlark nests were successful (i.e., fledged at least 1 young or young remained in the nest ≥8 days post-hatching). The amount of woody vegetation surrounding nest locations was significantly associated with daily nest survival of Grasshopper and Henslow's sparrows, and Eastern Meadowlarks (Beta estimate = -1.19 ± 0.457 SE; $\chi^2 = 6.57$, $P = 0.010$), despite all three species differing in daily nest survival rates (Beta estimates: Eastern Meadowlark = -1.55 ± 1.17 SE, Grasshopper Sparrow = -2.39 ± 1.13 SE,

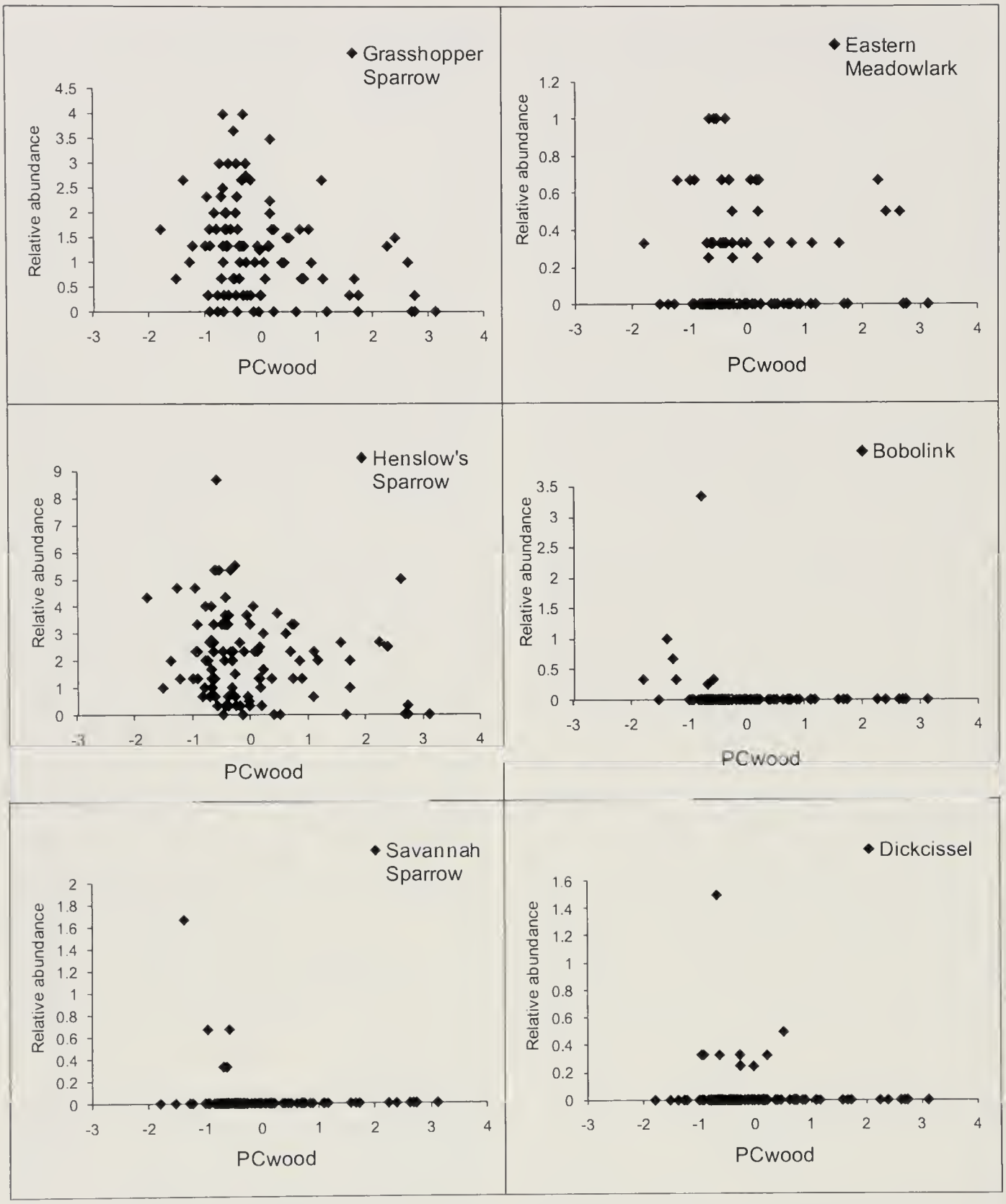

FIG. 1. Relative abundance of grassland bird species (A–F) within 100-m radius of 101 point-count locations on reclaimed surface mines in relation to amount of woody vegetation (PCwood) in eastern Ohio, 2005–2006. Amount of woody vegetation increases from −3 to 4 along the x axis.

Henslow's Sparrow = 0.00; $\chi^2 = 11.71$, $P = 0.003$). There was no evidence of significant interactions and all three species responded similarly to woody vegetation surrounding their nests ($\chi^2 = 4.32$, $P = 0.12$).

Mean ± SE daily nest survival rate was 0.76 ± 0.001 for Grasshopper Sparrows, 0.94 ± 0.020 for Henslow's Sparrows, and 0.87 ± 0.006 for Eastern Meadowlarks. Daily nest survival of Grasshopper and Henslow's sparrows was nega-

TABLE 1. Mean percent woody vegetation, number of woody patches, and distance to woodland edge (± SE) for nest-site locations of Grasshopper and Henslow's sparrows, and Eastern Meadowlarks and random vegetation plots.

	Grasshopper Sparrow			Henslow's Sparrow			Eastern Meadowlark			Random
Variable	$\bar{x}$ ± SE	*F*	*P*	$\bar{x}$ ± SE	*F*	*P*	$\bar{x}$ ± SE	*F*	*P*	$\bar{x}$ ± SE
% Woody vegetation	1.5 ± 0.29	5.4	0.021	2.3 ± 1.38	1.0	0.325	1.5 ± 0.64	2.2	0.137	4.0 ± 0.70
# Woody patches	3.1 ± 0.49	1.8	0.188	2.7 ± 1.04	1.4	0.233	1.9 ± 0.42	3.6	0.061	4.2 ± 0.51
Distance to woodland	165.3 ± 11.70	1.0	0.331	161.1 ± 16.09	0.7	0.396	201.8 ± 19.39	0.7	0.391	181.1 ± 9.49

tively associated with amount of woody vegetation (PCwood) surrounding nest locations (Fig. 2). Eastern Meadowlark daily nest survival was marginally associated with amount of woody vegetation in proximity to nest locations (Fig. 2).

DISCUSSION

Our findings suggest woody vegetation negatively influenced abundance, nest placement, and nesting success of some grassland bird species on reclaimed surface mines. Our results are consistent with previous studies of the effects of woody vegetation on grassland bird occurrence in the midwestern U.S.; however, our study is unique as we specifically examined reclaimed surface mines (but see Bajema et al. 2001 and Galligan et al. 2006). The abundance of obligate grassland birds has been shown to be negatively related to woody vegetation in Minnesota and North Dakota (Grant et al. 2004, Winter et al. 2006, respectively), southwestern Missouri (Winter and Faaborg 1999), Illinois (O'Leary and Nyberg 2000), eastern South Dakota (Bakker et al. 2002), and West Virginia (Wray et al. 1982). Our failure to detect an association between woody vegetation and abundance of Eastern Meadowlarks and Dickcissels was possibly an artifact of the relatively large territory size of these species and use of fixed radius sampling (detections >100 m were not included in the analysis).

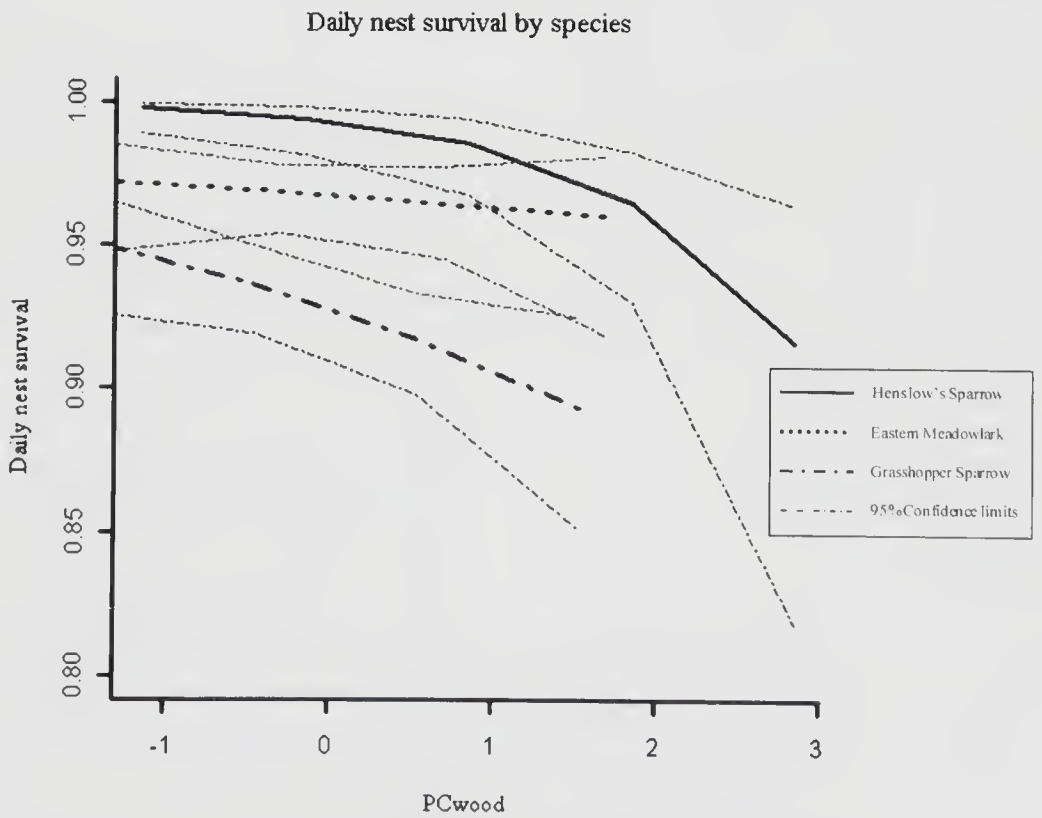

FIG. 2. Daily survival rates of Grasshopper and Henslow's sparrow, and Eastern Meadowlark nests in relation to amount of woody vegetation (PCwood) in proximity to nest-site locations at Tri-Valley and Woodbury Wildlife Management areas in eastern Ohio, 2005–2006. Amount of woody vegetation increases from −1 to 3 along the x axis.

Winter and Faaborg (1999) also found no significant association between woody vegetation and density of these two species. The small number of observations on surveys may have limited our ability to identify patterns in cases where we did not detect significant associations (e.g., Savannah Sparrow and Dickcissel).

Numbers of Grasshopper, Henslow's, and Savannah sparrows, and Bobolinks were negatively related to percent cover of woody vegetation within 100 m of survey locations, but only Grasshopper Sparrows showed strong evidence of selecting nest patches with lower amounts of woody vegetation than random locations. Our analysis failed to discriminate between Eastern Meadowlark and Henslow's Sparrow nests and random locations, perhaps because of small sample size (n = 18 nests) or the conservative nature of our comparison of used plots to random plots versus used plots to non-used plots. Nest locations of Eastern Meadowlarks had more than two times less woody cover and fewer woody patches within 100 m than random locations (Aldredge and Griswold 2006, Buskirk and Millspaugh 2006, Johnson et al. 2006, Thomas and Taylor 2006). The literature on effects of woody vegetation on nest-site selection of grassland birds has yet to reveal consistent relationships, and investigations show active avoidance of woody vegetation during nest-site selection of Eastern Meadowlarks, Henslow's and Grasshopper sparrows, and Dickcissels (Hull 2000, Winter et al. 2000, Hubbard et al. 2006), positive associations with trees for Grasshopper Sparrows (Sutter and Ritchison 2005), or no association between nest-site selection and presence of woody vegetation for Vesper and Clay-colored sparrows (Grant et al. 2006). Grassland nesting passerines may use the absence of woody vegetation as a cue during nest-site selection given that certain predators (i.e., mice) and brood parasites (i.e., Brown-headed Cowbird [*Molothrus ater*]) frequently use woody vegetation both as cover and visual perches (With 1994).

Daily nest survival was related to the amount of woody vegetation surrounding nests of Grasshopper and Henslow's sparrows and marginally related to Eastern Meadowlark nests, which is consistent with other studies conducted elsewhere in the Midwest (Winter et al. 2000, Scheiman et al. 2003, Bollinger and Gavin 2004, Davis 2005; but see Grant et al. 2006). Woody vegetation and woodland edges may support a diverse predator community not otherwise present in grassland systems (Renfrew and Ribic 2003). Woody elements are generally thought to attract predators because they provide perches for avian predators and promote use by other predators due to cover and other resources (Thompson and Burhans 2003, Renfrew et al. 2005).

We suggest efforts to remove woody vegetation will enhance the value of reclaimed surface mines for grassland birds given the apparent avoidance of woody vegetation and the overall low daily nest survival of Grasshopper Sparrows and Eastern Meadowlarks, coupled with results from other studies relating low nesting success to presence of woody vegetation. Removal of encroaching woody plants will increase grassland area and reduce edges and fragmentation. It may also decrease numbers of woodland predators by eliminating cover or perches and reducing movement corridors. This should make grassland units more productive and attractive to a diverse community of grassland-nesting birds. Our study emphasizes the role of woody vegetation in grassland bird management on reclaimed surface mines, but managers should also remain attentive to landscape and patch-scale issues given their known influence on grassland birds (Ribic and Sample 2001, Bakker et al. 2002, Winter et al. 2005).

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EFFECTS OF BREEDING STAGE AND BEHAVIORAL CONTEXT ON SINGING BEHAVIOR OF MALE INDIGO BUNTINGS

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ABSTRACT.—We studied the effects of breeding stage and behavioral context on the singing behavior of male Indigo Buntings (*Passerina cyanea*; $n = 15$) during the 2004 breeding season in Madison County, Kentucky, USA, to better understand how males with a single-song repertoire vary the characteristics of their song to convey different information. Playback experiments were conducted in 2005 in territories of focal males ($n = 14$) to further examine the possible effect of male-male interactions on singing behavior. We analyzed 10,919 songs of 15 male Indigo Buntings with songs consisting of a series of figures that were usually paired (i.e., phrases). Mean song duration was 2.30 ± 0.13 (SE) sec (range = 1.44–3.40 sec) with males varying song duration by varying the number of figures and phrases in each song. Singing rates varied significantly ($P < 0.0001$) among breeding stages and were highest prior to pairing, suggesting singing has a role in mate attraction. Singing rates also differed ($P = 0.013$) during playback experiments with rates higher during playback and post-playback periods ($\bar{x} = 4.4$ songs/min) than during the pre-playback period ($\bar{x} = 2.9$ songs/min). These results suggest that singing also has a role in territory defense. Songs of male buntings tended to be shorter prior to pairing and were generally longer in duration after pairing. Playback experiments revealed that bunting songs were longer ($P = 0.03$) during and after playback ($\bar{x} = 2.6$ sec) than during the pre-playback period ($\bar{x} = 2.0$ sec). These results suggest male Indigo Buntings vary singing rates and song duration to convey different information, appearing to use shorter songs uttered at high rates to attract mates and longer songs to convey aggression during male-male interactions. *Received 21 December 2009. Accepted 3 June 2010.*

Males of most species of passerines have multi-song repertories (MacDougal-Shackleton 1997). These repertoires may be important in male-male interactions (song matching; Stoddard et al. 1992), preventing habituation (Krebs et al. 1978, Yasukawa 1981), providing information about motivational state (Falls 1969), and repelling intruders (Krebs et al. 1978, Yasukawa 1981). Song repertoires may also have intersexual functions. For example, female Atlantic Canaries (*Serinus canaria*) exhibit more nest building behavior when subjected to playback of larger repertoires (Kroodsma 1976).

Males of some species, such as Ovenbirds (*Seiurus aurocapilla*; Weary and Lemon 1988) and Henslow's Sparrows (*Ammodramus henslowii*; Leftwich and Ritchison 2008), have a single song type. Males with single-song repertoires could potentially use singing to convey different information, but may do so by altering the characteristics of their single song (Morton and Young 1986, Leftwich and Ritchison 2008). However, few investigators have examined how male songbirds with single-song repertoires vary their singing behavior or the characteristics of their songs during the breeding season and in different behavioral contexts.

Male Indigo Buntings (*Passerina cyanea*) have a repertoire of one song type or theme (Payne 2006), and little is known about how their singing behavior varies during the breeding season and in different social contexts (Thompson 1972, Shiovitz 1975). We examined the effects of breeding stage and behavioral context on their singing rates and singing behavior to better understand (1) the possible functions of singing by male Indigo Buntings, and (2) how males with a single-song repertoire might vary their singing behavior to convey different information.

METHODS

We studied Indigo Buntings from 26 April to 20 August 2004 and 19 May to 5 June 2005 at the Central Kentucky Wildlife Management Area, 17 km southeast of Richmond, Madison County, Kentucky, USA. Male buntings were observed and recorded in 2004, and playback experiments were conducted in 2005. The study area consisted primarily of wooded edges, scattered trees, and fields in early stages of succession. Male buntings were captured using playback of conspecific songs to lure them into mist nets. Captured buntings were banded with a U.S. Geological Survey aluminum band plus a unique combination of three colored plastic bands to aid in individual recognition. Male age (second-year [SY] or after-second-year [ASY]) was assigned using plumage differences (Pyle 1997, Payne 2006).

Territory boundaries were delineated by monitoring movements of focal males and noting

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locations of interactions with conspecifics. Focal individuals were observed and recorded 2–3 times per week during observation periods of 20–30 min. All observations were conducted during the period from just after sunrise to 1100 hrs (EDT) when singing rates of Indigo Buntings are relatively constant (Thompson 1972). Inclement weather may influence singing behavior so buntings were not observed when it was raining. The date, time, and focal bird's identity were noted on tape prior to each session. Recordings were made using a Sony (TCM-50DV) cassette recorder with a Sennheiser shotgun microphone (Model ME 88), typically at a distance of 10–30 m from focal males.

All songs of focal males were recorded during each observation period and the breeding stage was noted. Songs were categorized during each observation, as: (1) spontaneous advertising (no conspecific males heard or observed), (2) long-range interaction, where a conspecific male was singing in an adjacent or distant territory ≥50 m away, and (3) short-range interaction, where a conspecific male was singing <50 m away. Focal male songs were classified as long- and short-range up to 1 min after a conspecific was last heard singing.

We divided the breeding season into six stages: (1) pre-pairing (no female present on male's territory), (2) nest building (period of nest construction by the female), (3) egg-laying (from the day the first egg was laid to the day the penultimate egg of a clutch was laid), (4) incubation (from the day the last egg was laid to the day before first egg hatched), (5) nestling (from the day the first egg hatched to the day before young fledged), and (6) post-fledging (from the day the young leave the nest to the time when fledglings leave male's territory). Female buntings frequently produce two broods during the breeding season and often began new nests several days after young from a previous nest fledged. Thus, the post-fledging period ended when a female began building a new nest.

An attempt was made to locate and monitor all nests in the territories of focal males to identify breeding stages. Nests were located by observing movements of females during nest building and nestling provisioning, and by searching likely nest sites in focal territories. Nests were found at several stages and we, at times, backdated to ascertain the dates of breeding stages. We used the following durations for backdating: 8 (first nest of the season) or 2 (later nests) days for nest building, 1 day for each egg in a clutch for egg laying, 12 days for incubation, and 9 days for the nestling period (Bradley 1948, Payne 2006).

Playback experiments were conducted in 2005 in territories of focal males (n = 14) to further examine the possible effect of male-male interaction on the singing behavior of male Indigo Buntings. All songs used for the playback experiments were taken from commercially-available recordings (*Common Birds and Their Songs*, Houghton Mifflin Company; *More Birding by Ear —Eastern/Central*, Houghton Mifflin Company, Boston, MA, USA). Three tapes, each with songs of a different male, were used in the experiments (Tape 1 means: song length = 1.8 sec, number of figures = 4.3, number of phrases = 5.3; Tape 2 means: song length = 2.9 sec, number of figures = 12.5, number of phrases = 7.5; Tape 3 means: song length = 2.8 sec, number of figures = 14.7, number of phrases = 9.3; definitions of figure and phrase are below). Tapes 1, 2, and 3 had three, four, and three different versions of each male's song, respectively. Male buntings on all three tapes sang at a rate of four songs/min. Recordings of males singing at higher rates would have increased the probability of the songs of focal males overlapping those on the recordings, making subsequent song analysis more difficult. A speaker was placed near the center of the focal male's territory to simulate singing by an intruding male during each experiment. Each experiment consisted of a 3-min pre-playback period and a 6-min playback/post-playback period (with songs played back for 3 min and observations continuing for an additional 3 min after playback ended).

All songs recorded during each observation period were analyzed. Characteristics of songs measured included song duration, number of figures ("a sound which produces a single, complete, and distinct impression uninterrupted by silence greater than two centiseconds"; Shiovitz 1975:133), and the number of phrases ("a subdivision of a song based upon recognizable groups of sequential figures"; Shiovitz 1975:133; Fig. 1). In addition, we noted if songs had "squeaky" notes added or were uttered at higher than normal volume during the playback experiments. High-frequency "squeaky" notes are occasionally inserted between phrases in songs of male Indigo Buntings during territorial disputes (Emlen 1972, Thompson 1972, Margo-

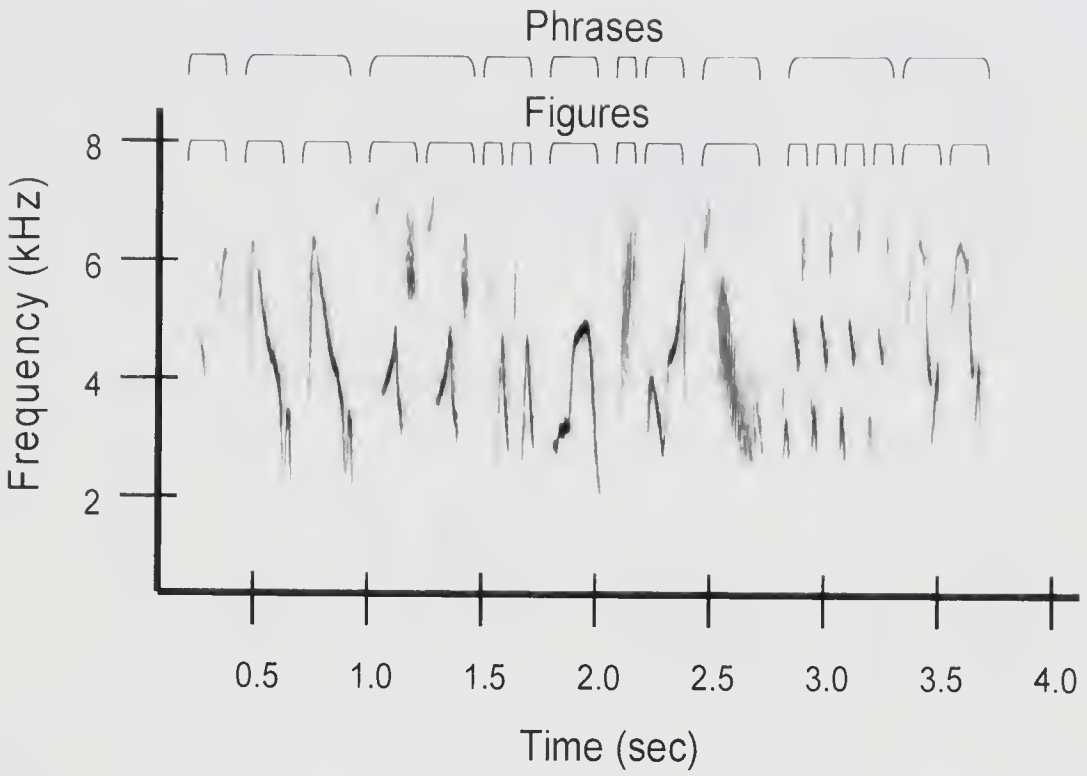

FIG. 1. Spectrograph of a typical song of a male Indigo Bunting showing the terminology used.

liash et al. 1994). Song volume was subjeetively eategorized as either normal or high volume. We attempted to maintain a eonstant distanee from foeal males during playbaek experiments to permit better estimation of song volume. Reeordings of the songs of foeal males were subsequently analyzed using sound-analysis software (Raven Version 1.2.1, Cornell Laboratory of Ornithology, Ithaea, NY, USA).

Possible variation in eharaeteristies of songs of male Indigo Buntings with male age, breeding stage, and behavioral eontext were examined using repeated measures analysis of varianee with Student-Newman-Keuls (SNK) *post-hoc* tests to examine possible differenees among means. All analyses were eonducted using the Statistieal Analysis System (SAS Institute 1999). All values are presented as mean ± standard error. Mean values were ealeulated using the means for eaeh foeal male to avoid bias due to different sample sizes.

RESULTS

We found no differences in eharaeteristies of songs of SY and ASY male Indigo Buntings (song duration, number of figures, and number of phrases; all $P \geq 0.17$). Thus, songs of all males (SY and ASY) were eombined for subsequent analyses.

All male Indigo Buntings ($n = 15$) in our study had a repertoire of a single song type. Mean song duration was 2.30 ± 0.13 see and the mean number of figures per song was 9.95 ± 0.51. The mean number of phrases per song was 6.15 ± 0.46.

Songs of male buntings exhibited both intra- (Fig. 2) and inter-individual (Fig. 3) variation. Eaeh male had a typieal song that ineluded a series of figures (phrases), usually paired, and usually uttered in the same order. The number of figures in eaeh phrase oeeasionally varied, and figures (phrases) typically used later in songs were often omitted (Fig. 2).

Songs of some males (5 of 15, 33%) were unique and shared few or no song figures with other males. Males in adjaeent territories typically shared some and, at times, all of the figures used in their songs and formed song neighborhoods where males used either the same or similar song figures (10 of 15, 67%; Fig. 4). One SY male in our study altered his song shortly after arriving in the study area (Fig. 5).

Effects of Breeding Stage and Natural Interactions on Singing Behavior.—Singing rates (songs/min) of male Indigo Buntings varied signifieantly among breeding stages ($F_{5,45} = 15.1$, $P < 0.001$) with rates highest during the pre-pairing stage (SNK test, $P < 0.05$; Fig. 6). Singing rates during the other breeding stages (nest-building, egg-laying, ineubation, nestling, and post-fledging) did not differ (SNK test, $P > 0.05$; Fig. 6).

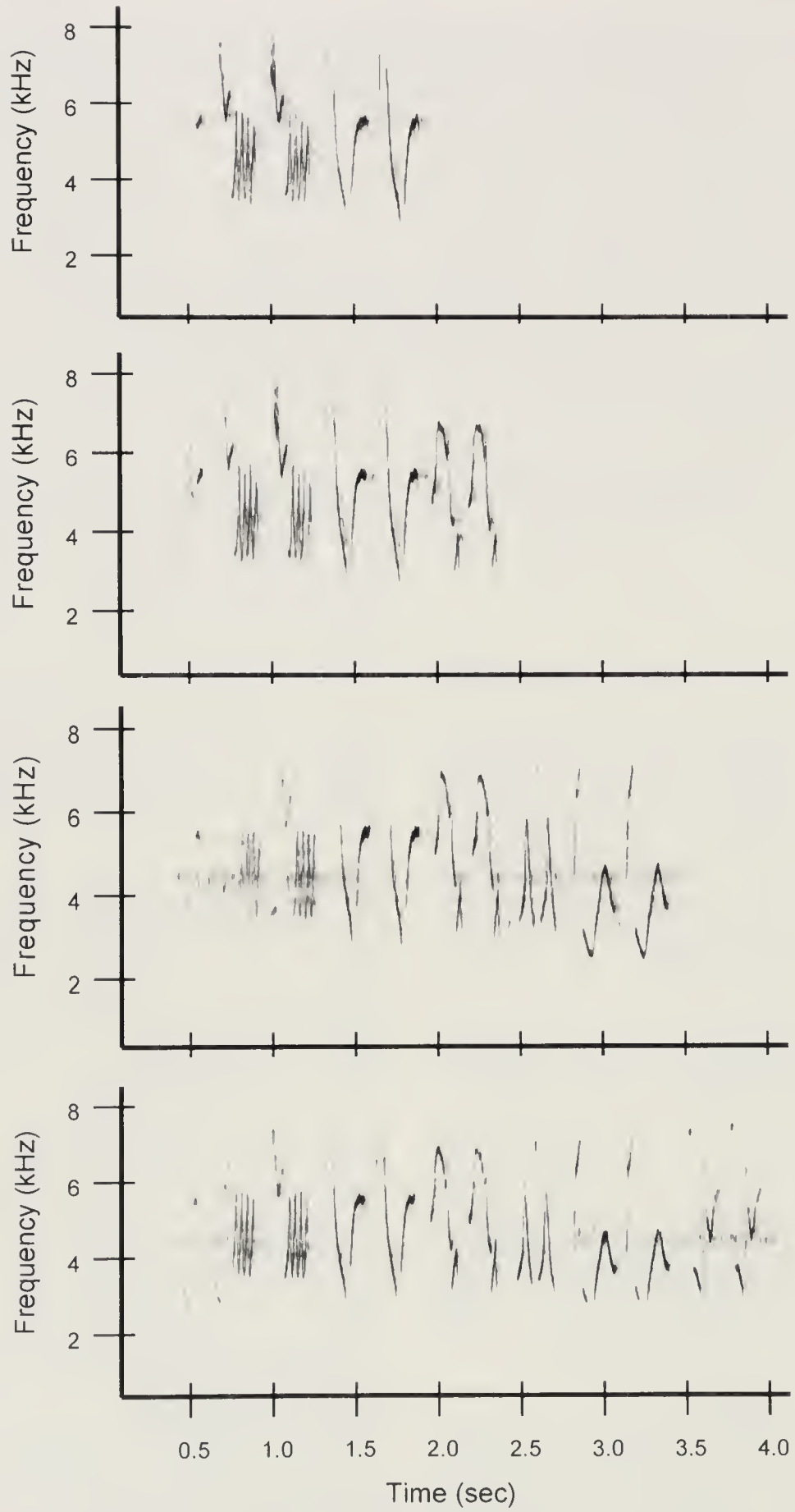

FIG. 2. Spectrographs illustrating the typical variation that exists in the single song of a male Indigo Bunting.

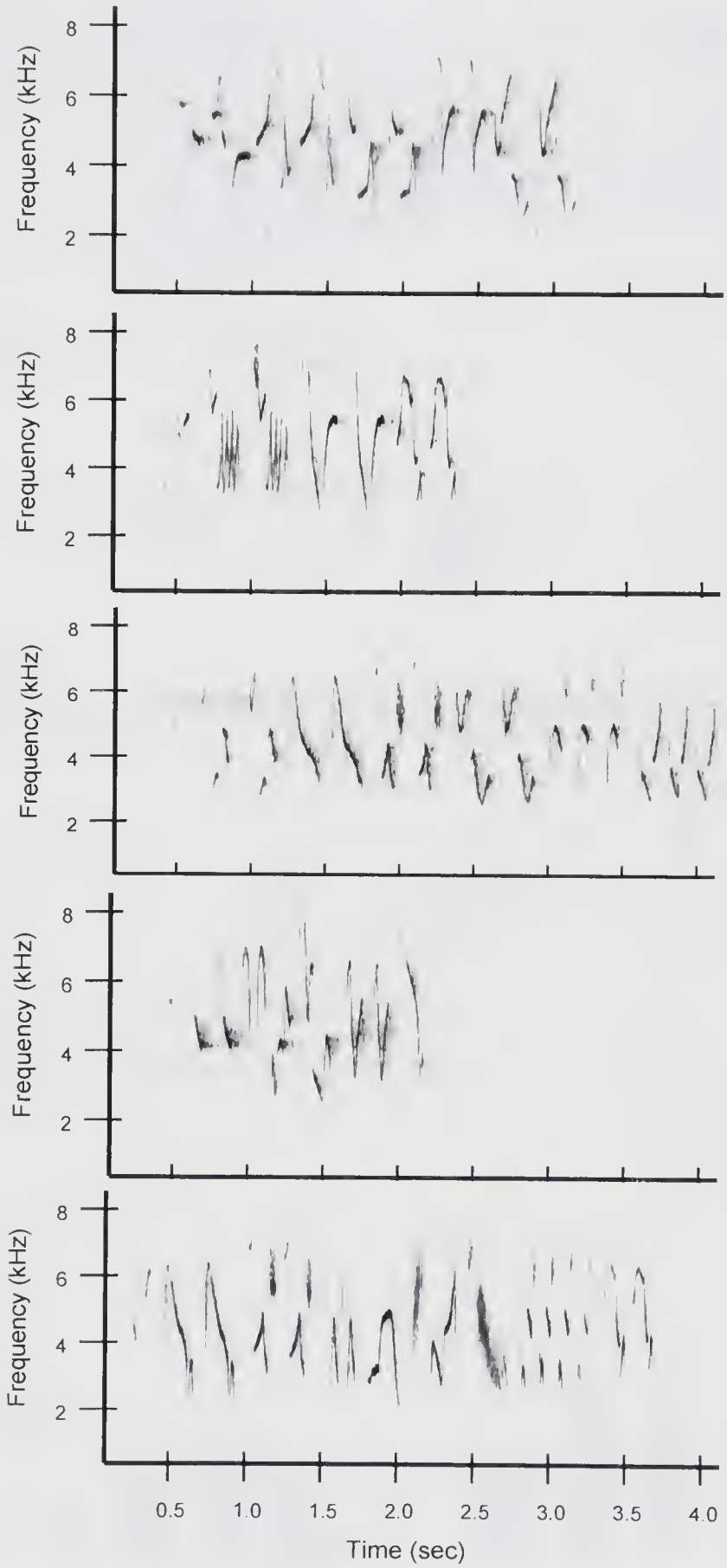

FIG. 3. Spectrographs illustrating the typical variation among songs of different male Indigo Buntings.

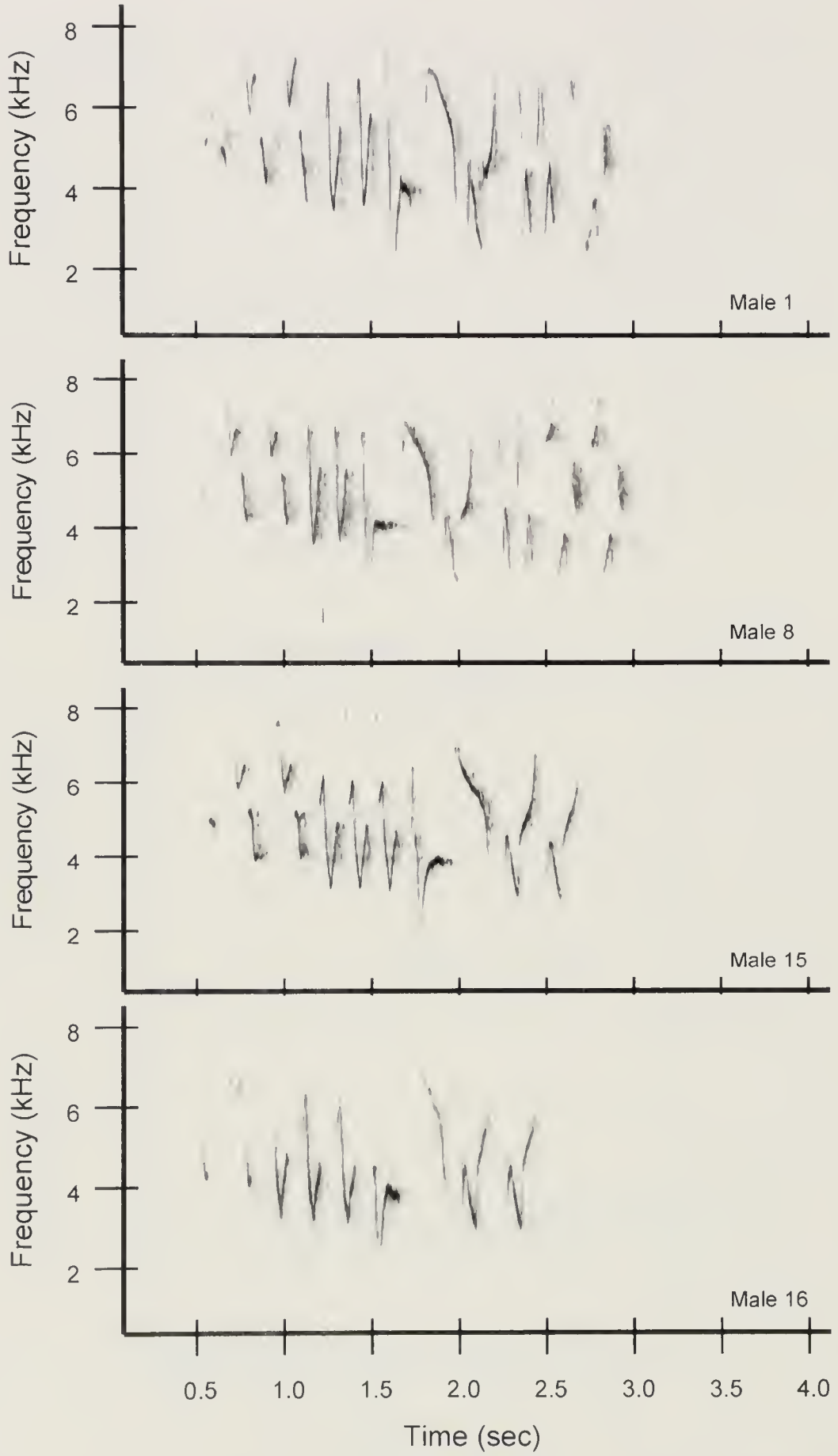

FIG. 4. Spectrographs illustrating the close matching of songs of several neighboring male Indigo Buntings in a song neighborhood.

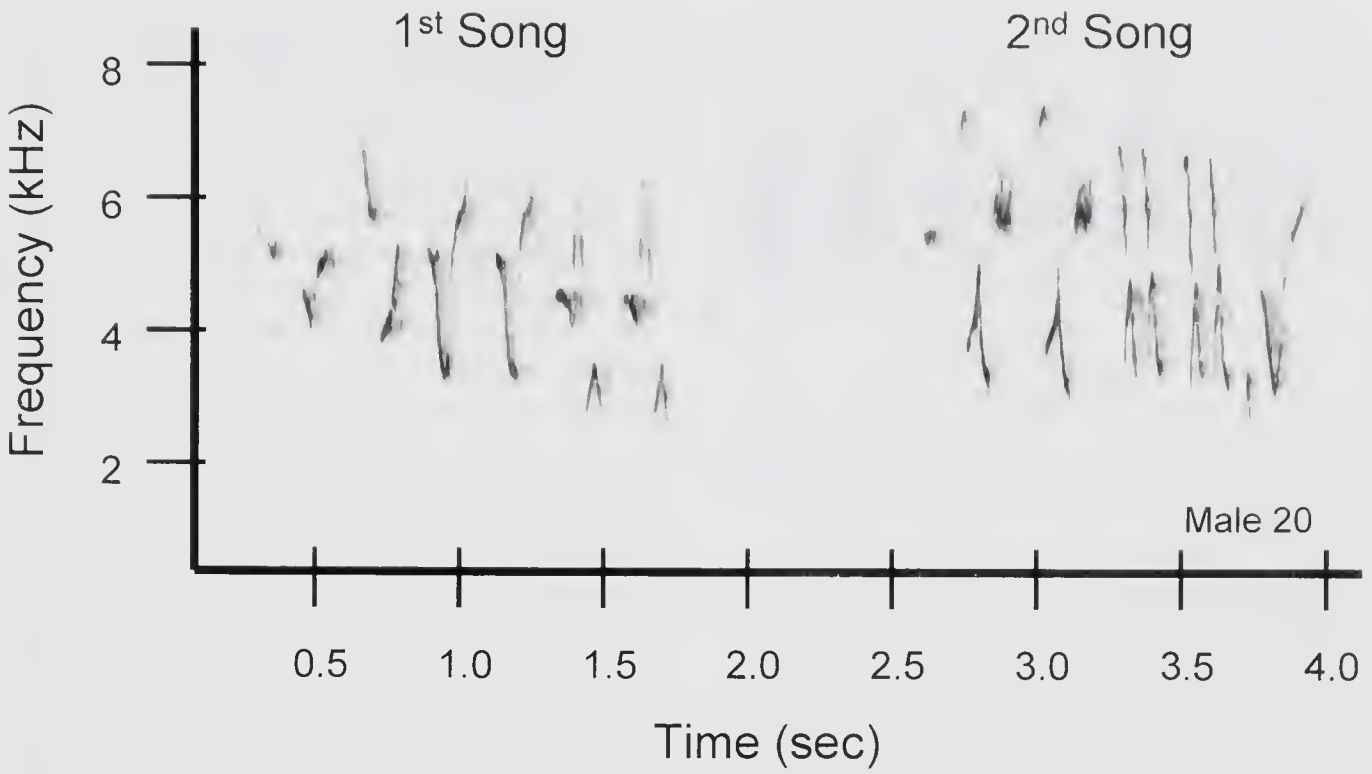

FIG. 5. Spectrographs of two songs uttered by a second-year (SY) Indigo Bunting male illustrating song switching. The first song was used immediately after arrival on his territory. Several days later, the second song incorporated figures and phrases from those of a neighboring male.

Differences in the mean duration of songs uttered by male Indigo Buntings during different breeding stages approached significance ($F_{5,31}$ = 2.2, P = 0.075) with longer songs during the nest-building period (Fig. 7). Songs were shorter in duration during post-fledging and pre-pairing periods than during other breeding stages (Fig. 7).

Differences among breeding stages in the mean number of figures ($F_{5,31}$ = 2.1, P = 0.099) and phrases ($F_{5,31}$ = 2.1, P = 0.094) per song also approached significance with more figures and phrases per song during nest-building and egg-laying stages and fewer during post-fledging and pre-pairing stages (Fig. 8). None of the characteristics of songs of male buntings, including duration and number of figures and phrases per song differed among behavioral contexts (short-range interaction, long-range interaction, or spontaneous singing; $P \geq 0.24$).

Effects of Song Playback on Singing Behavior.—We compared singing behavior of male Indigo Buntings prior to presentation of the stimulus (pre-playback period) to that during and after presentation of the stimulus (playback and post-playback periods combined). Singing rates (songs/min) differed ($F_{1,10}$ = 8.3, P = 0.013) between periods with higher rates during the

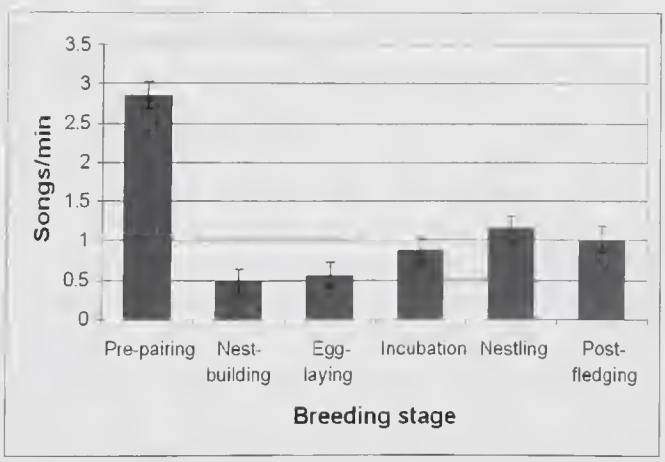

FIG. 6. Mean singing rates (± SE) of male Indigo Buntings during different breeding stages.

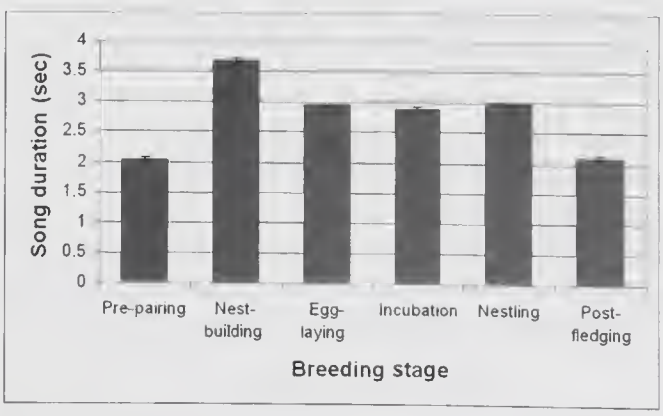

FIG. 7. The mean duration of songs (± SE) uttered by male Indigo Buntings during different breeding stages.

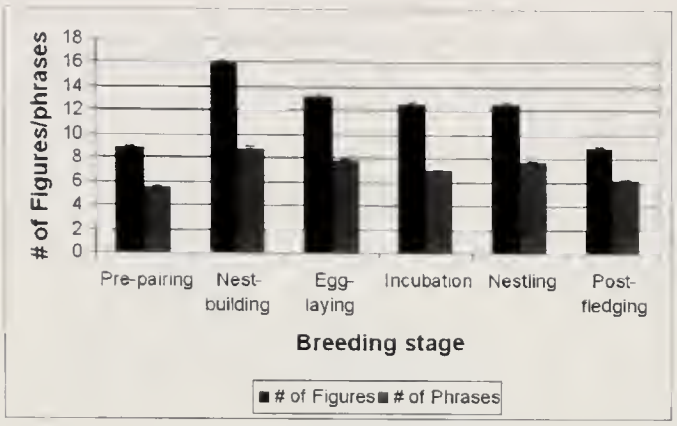

FIG. 8. Mean number of figures and phrases (± SE) in songs of male Indigo Buntings during different breeding stages.

playback and post-playback periods ($\bar{x}$ = 4.4 ± 0.4 songs/min) than during the pre-playback period ($\bar{x}$ = 2.9 ± 0.6 songs/min). The characteristics of songs also differed between periods with longer songs ($F_{1,10}$ = 6.4, P = 0.03) that included more figures ($F_{1,10}$ = 6.6, P = 0.028) and phrases ($F_{1,10}$ = 5.0, P = 0.049) uttered during and after playback ($\bar{x}$ duration = 2.6 ± 0.1 sec; $\bar{x}$ number of figures = 11.4 ± 0.1; $\bar{x}$ number of phrases = 6.8 ± 0.2) than prior to playback ($\bar{x}$ duration = 2.0 ± 0.1 sec; $\bar{x}$ number of figures = 8.8 ± 0.4; $\bar{x}$ number of phrases = 5.5 ± 0.2). Male buntings also uttered a significantly higher percentage ($F_{1,10}$ = 6.3, P = 0.026) of high-volume songs during the post-presentation period ($\bar{x}$ = 11.4 ± 3.7%) than the pre-presentation period (none uttered). Comparison of pre- and post-presentation periods revealed no difference in use of songs including high-frequency 'squeaky' notes ($F_{1,10}$ = 0.02, P = 0.9).

DISCUSSION

Song Matching.—All male Indigo Buntings in our study had a repertoire of one song type. Songs of some male buntings were unique, as also noted by previous investigators (Thompson 1970, Payne et al. 1988). Most males with adjacent territories in our study shared some, if not all, of the figures in their songs with conspecifics, and formed song neighborhoods where males in adjacent territories used the same or similar song figures. Song neighborhoods have been reported in other populations of Indigo Buntings (Thompson 1970, Payne and Westneat 1988). Song neighborhoods may develop because incorporating figures used by resident males into their songs may be beneficial for young male buntings with SY males that song match more likely to successfully acquire and defend a territory, acquire a mate, and fledge young (Payne 1982, 1983).

Song Function.—Our results indicate singing by male Indigo Buntings functions in mate attraction with singing rates declining significantly after pairing. Thompson (1972) also reported male Indigo Buntings sang more songs per bout and more bouts/hr when unmated. Previous studies suggest male singing rates represent a performance-related trait under positive sexual selection (Gil and Gahr 2002) that can influence mate choice and timing of mate acquisition (Alatalo et al. 1990, Hoi-Leitner et al. 1995). Otter et al. (1997) reported that singing rates represented accurate signals of male quality in Black-capped Chickadees (*Poecile atricapillus*). Singing rates of male buntings and males of other species of songbirds (e.g., Albrecht and Oring 1995, Ritchison 1995, Balsby 2000) decline after pairing. Thus, high singing rates prior to pairing may provide females with information concerning male status (paired or not) and their quality.

Male Indigo Buntings in our study continued singing after pairing, but at lower rates. Singing by male buntings, both before and after pairing, as for males of many species of songbirds (e.g., Krebs et al. 1978, Nowicki et al. 1998), is likely important in territorial defense. Male Indigo Buntings typically arrive in breeding areas ~1–2 weeks before females (Payne 2006; GR, pers. obs.) and establish breeding territories. During this period, and throughout our study, males were at times observed counter-singing with neighboring males and chasing conspecifics near territory boundaries while singing; males responded to playback by increasing their singing rates. These observations indicate that singing by male Indigo Buntings has an important role in establishing and defending territories.

Singing rates of male Indigo Buntings in our study were lowest during the fertile periods of their mates (nest-building and egg-laying periods) and remained relatively low during the incubation, nestling, and post-fledging periods. Some investigators have suggested singing may be important for stimulating female reproductive cycles (Hinde and Steel 1976) or guarding mates (Møller 1988). Singing by male Indigo Buntings does not appear to serve these functions because singing rates in our study were lowest during female fertile periods. Males of most songbird species do not sing or sing at low rates during the fertile periods of their mates (Gil et al. 1999).

Song Characteristics.—Songs of male Indigo Buntings in our study tended to be shorter prior to pairing and were generally longer in duration after pairing. In addition, bunting songs were significantly longer during and after playback than during the pre-playback period. These results suggest male Indigo Buntings may use shorter songs to attract females, and longer songs to convey aggression during male-male interactions. Although females in some species appear to prefer males that sing longer songs (e.g., White-throated Sparrows, *Zonotrichia albicollis*; Wasserman and Cigliano 1991), females in other species prefer males that sing at faster rates (e.g., European Pied Flycatcher, *Ficedula hypoleuca*; Gottlander 1987, Alatalo et al. 1990). If mate choice decisions by female Indigo Buntings are influenced by singing rates, then one possible explanation for the tendency of males to sing shorter songs prior to pairing is that such songs allow males to sing at higher rates (i.e., more songs per unit time). In addition, however, given that longer songs appear to convey an increased tendency for aggression, male buntings may also sing shorter songs prior to pairing to signal their non-aggressive intentions to potential mates. Similarly, Staicer (1996) suggested that male Adelaide's Warblers (*Dendroica adelaidae*) may use songs with characteristics that convey less aggression ('appeasing songs') during interactions with females.

Male buntings in our study often added additional phrases to their songs during encounters with other males, both in response to playback and when chasing conspecifics. Emlen (1972) noted that buntings used 'lengthened' songs during agonistic encounters, and Saunders (1929:48) witnessed "male Indigo Buntings chasing each other about from tree to tree, and both of them singing prolonged songs in flight." In addition, Shiovitz (1975) found that playback of long variations of songs elicited stronger responses by male buntings than shorter variations. Shiovitz (1975) also suggested the first few figures of the songs of male buntings likely functioned as a "sign on" in gaining the attention of conspecifics, whereas the remainder of the song seemed to convey aggression. Thus, male Indigo Buntings appear to increase song duration to convey aggression, and perhaps the likelihood of interacting, during intrasexual encounters. Males of other species also appear to use longer songs to convey an increased likelihood of aggression during intrasexual encounters (e.g., McGregor and Horn 1992, Balsby and Dabelsteen 2001, Leitao et al. 2006, Lattin and Ritchison 2009).

We found male Indigo Buntings at times added 'squeaky notes' to songs and sang with increased volume during male-male interactions. Thompson (1972) also indicated male Indigo Buntings inserted high-frequency (about 9 kHz), 'squeaky' notes into songs when an intruding male was present in a territory. Emlen (1972) noted that male buntings at times added high-pitched 'squeak' notes when responding aggressively to playback of conspecific songs. These results suggest male buntings alter the characteristics of their single song to convey an increased likelihood of aggression, i.e., singing longer, louder songs that at times include 'squeaky' notes. In further support of this hypothesis, male buntings in our study at times inserted high-frequency 'squeaky notes' into songs during territorial chases with conspecifics and uttered songs at higher than normal volume when countersinging at territory boundaries (MDB and GR, pers. obs.). Changes in characteristics of songs during intrasexual encounters have also been reported in other species of songbirds. For example, male Barn Swallows (*Hirundo rustica*) emphasize 'rattles' in their songs during aggressive encounters, indicating that 'rattles' are an important component of competitive interactions between males (Galeotti et al. 1997). Similarly, American Pipits (*Anthus rubescens*) incorporate 'snarr' notes, a rasping element with a broad frequency range, into their songs during territorial disputes (Rehsteiner et al. 1998).

Our results suggest the single song type of male Indigo Buntings serves several functions, including mate attraction and territory defense. In addition, male buntings vary song rates and song duration during the breeding season and in different behavioral contexts, appearing to use shorter songs uttered at high rates to attract mates and longer songs to convey aggression during male-male interactions.

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DEVELOPMENT OF INCUBATION TEMPERATURE AND BEHAVIOR IN THRUSHES NESTING AT HIGH ALTITUDE

MARTIN L. MORTON[1,2] AND MARIA E. PEREYRA[1]

ABSTRACT.—Onset of incubation was studied in three Hermit Thrushes (*Catharus guttatus*) and one American Robin (*Turdus migratorius*), all with four-egg clutches, at a high altitude site in the Sierra Nevada, California, USA. Behavior of laying females at the nest was measured from continuous recordings of internal egg temperatures of first-laid eggs. Full nocturnal nest attentiveness began immediately with the first egg. Daytime attentiveness increased steadily during laying as foraging time away from the nest decreased. On-off bouts by tending females in daytime increased in frequency and decreased in duration until the last egg was laid. Time on the nest could not be directly equated to occurrence of incubation because eggs were not uniformly warmed to exceed the temperature threshold required for embryonic development (physiological zero). Incubation began, both day and night, after laying of the second egg. It increased steadily thereafter with percentage of daytime devoted to incubation lagging well behind that of nighttime. Nest attentiveness and incubation temperatures reached maxima about the time of clutch completion and were continued during following days. *Received 17 December 2009. Accepted 2 April 2010.*

Development of nest-attentiveness and incubation behaviors in female birds is a physiologically-driven process that begins during pre-laying and laying periods as females spend progressively greater amounts of time on the nest, and less time in foraging or other outside activities. The actual onset of the incubation phase, in which eggs reach temperatures sufficiently high to sustain embryonic development, corresponds with development of a functional brood patch and sustained application of heat to the eggs.

The rate at which these behaviors develop is influenced by underlying physiological mechanisms associated with gonadal maturation, follicular development and ovulation, and subsequent morphological changes with the appearance of a functional incubation patch. Subsequent behaviors surrounding the start of a clutch, although in large part driven by gonadal development initially stimulated by lengthening days (Wingfield 1984, Sharp et al. 1998, Dawson 2008), can be modulated by environmental conditions including availability and suitability of nest sites (Morton 1978, 2002), food supply (Hahn et al. 1995) and, in montane settings, storms (Morton 2002, Hahn et al. 2004). Once egg laying begins, the transition from laying to incubation progresses in an orderly fashion under the influence of a changing hormonal environment that eventually becomes dominated by prolactin (Vleck 1998).

The development of incubation behavior marks the transition between pre-nesting and maternal phases of reproduction, and is usually considered to occur gradually (Haftorn 1978, 1981, 1988; Zerba and Morton 1983; Oppenheimer and Morton 2000; Wang and Weathers 2009). Because embryonic development does not occur until eggs are warmed above a threshold of 25–27° C (White and Kinney 1974), termed the physiological zero temperature (PZT), the amount of time the female applies heat during laying, and prior to completion of a clutch, becomes a critical determinant of embryonic growth, the length of the incubation period, and subsequent amounts of hatching asynchrony within a clutch (Mead and Morton 1985). Much importance has been attached to the age-size hierarchy of hatchlings and many hypotheses have been advanced to explain its assumed adaptive value (Clark and Wilson 1985; Stoleson and Beissinger 1995, 1999). The widespread occurrence of hatching asynchrony and potential for maternal shifts in timing of incubation onset to exaggerate or suppress age-size hierarchies in hatchlings makes accurate measurements of events that accompany shifts in nest attentiveness between laying and incubation particularly important.

We demonstrate using egg temperature (Tegg) data from two species of thrush (Turdidae) that, although daytime attentiveness is frequently used in ecological studies to mark the start of the incubation period (and hence embryonic development), these are not equivalent conditions. In particular, we show the behavioral (daytime and night-time attentiveness) and physiological components of incubation (heat application) are decoupled early in laying, and only gradually

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converge into actual incubation, as defined by the maintenance of eggs at temperatures above the threshold for development.

METHODS

Nests from three Hermit Thrushes (*Catharus guttatus*) and one American Robin (*Turdus migratorius*) were used in a study conducted at Tioga Pass (37.8° N, 119.2° W; 3,000 m asl), in the Sierra Nevada, California, USA. All nests were in lodgepole pine (*Pinus contorta*). We inserted the tip of a 36-ga copper-constantan thermocouple into the center of the first egg within a few hours after it was laid, then glued the insulated leads to the shell. Lead wires were threaded through the nest bottom and connected to a hidden strip-chart recorder set to move at 2 cm/hr and calibrated to record between −5 and 45° C over a chart width of 10 cm. We moved well away from the nest during thermocouple installation (about 30 min), but left behind a dummy egg of the size and coloration of the thrush egg in case the laying female returned. Air temperature (Ta) was measured with a hygrothermograph placed in a vented box, in the shade, near the base of the nest tree. Temperature data for both Tegg and Ta were collected during the first 10 days of June in 1982 or 1985. Each nest was visited daily for quick inspections of nest contents and of the recording equipment.

RESULTS

All four thrushes laid three additional eggs on successive days after the first egg was implanted. Tegg data indicated that none of the birds returned to their nests on the first day (Day 1) until after sunset (Fig. 1). They remained on the nest throughout the night (~8 hrs) then left, presumably to forage, before returning to lay their second egg. One individual (Fig. 1A), for example, first returned to her nest on Day 1 at 2001 hrs PST, remained there for the entire night and left at 0356 hrs to begin Day 2. She was away from the nest for 268 min then began an attentive period at 0824 hrs. She laid the second egg during the next 168 min and made three on-off bouts before leaving the nest until 1945 hrs when night-time attentiveness was resumed. Behavior at the nest was much the same on Day 3 except the daytime attentive period began earlier (0754 hrs) and lasted longer (366 min). Continuous daytime attentiveness by the female on Day 4 began at 0936 hrs whereupon she laid her fourth egg, but left the nest thereafter only for relatively brief periods of foraging; full time attentiveness, both day and night had begun. Our method did not permit us to record time spent on the nest by females laying their first egg, but it can be deduced (Fig. 1) that daytime attentiveness increased with laying order. The same pattern of long periods away from the nest on laying days (Fig. 1A), also occurred in the other two Hermit Thrushes (Fig. 1B, C) except that one female (B) omitted the lengthy afternoon period of foraging a day earlier. The American Robin exhibited an attentiveness pattern during laying that resembled Hermit Thrushes. She was on the nest full time at night after the first egg was laid, but did not continue with an extensive late afternoon absence after Day 2 or in the early morning after Day 3 (Fig. 1D).

Females of both species did not sit on the nest continuously throughout their daytime periods of nest attentiveness (hatched bars), but left periodically to feed, as indicated by a sawtooth pattern to Tegg tracings. Frequency of these feeding or on-off bouts increased as laying proceeded and stabilized once the birds were in full-time incubation (Table 1).

Night-time attentiveness ended before sunrise as indicated in the four mornings shown for each bird (Fig. 1A, B, C, D). It ended 48.3 ± 11.5 min ($\bar{x}$ ± SD) before sunrise for the three Hermit Thrushes, and 27.2 ± 5.2 min for the American Robin. Night-time attentiveness resumed after sunset for the five nights shown. The mean was 36.2 ± 8.5 min after sunset for Hermit Thrushes and 44.2 ± 5.2 min for the American Robin. A Hermit Thrush, on the day of her first egg, settled for the night at 1824 hrs, nearly an hour before sunset (Fig. 1C, Day 1) when a storm with hail and cold rain occurred.

Females were on their nests during the first night after laying had begun, but chart recordings of Tegg indicated they were applying only enough heat to keep the egg between Ta and the threshold for development (Fig. 2). There was no daytime nest attentiveness following egg laying on the first day. Time spent on the nest increased as laying proceeded (shown for 2 days later, Fig. 3A) and females began to exhibit rhythmic on-off bouts during which time eggs were at times warmed above PZT. Neglect of eggs still occurred for considerable periods in daytime. For example, Day 3 (Fig. 3A) began with the female's departure at 0348 hrs (arrow 1) and during the

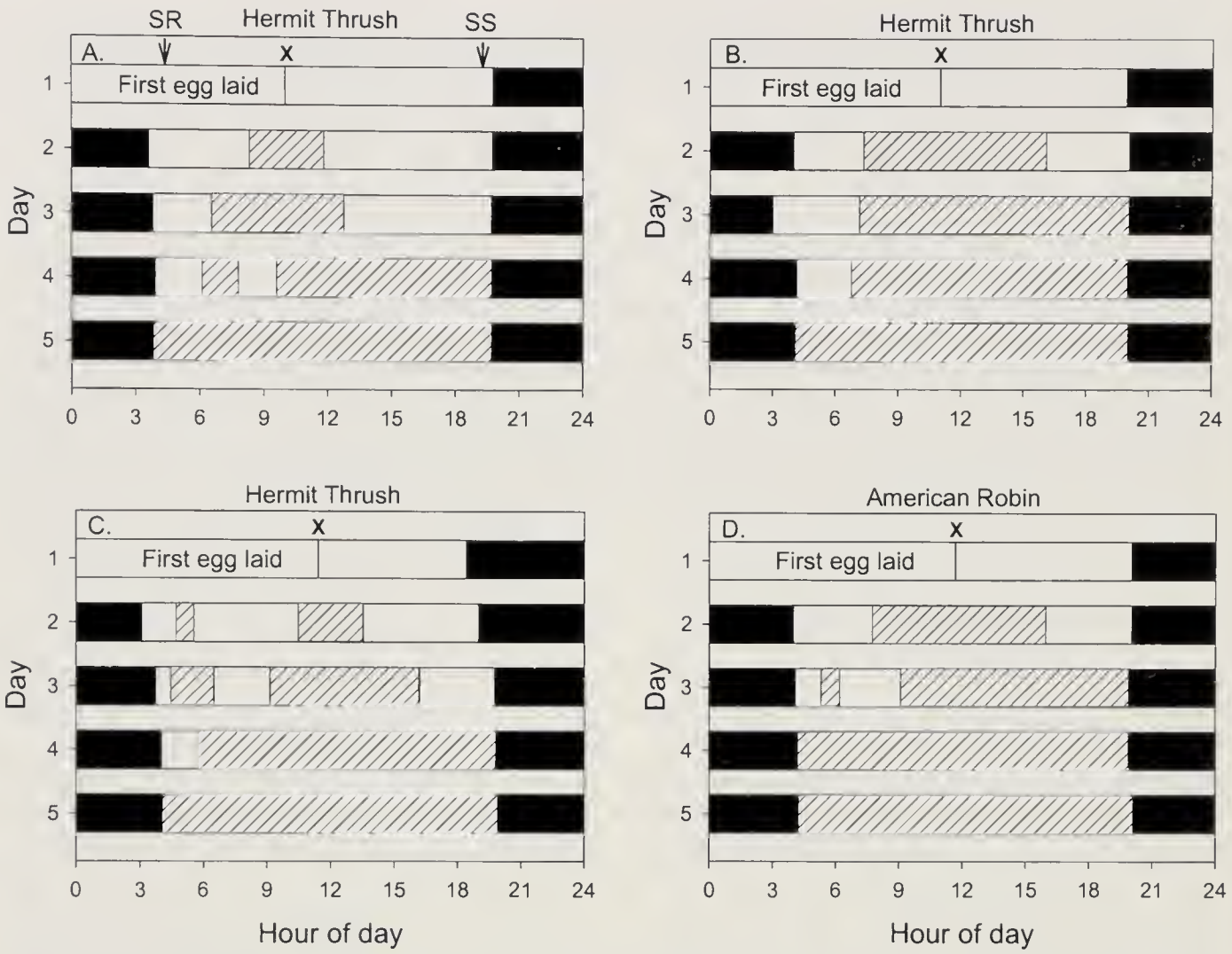

FIG. 1. Representation of nest attentiveness at Tioga Pass, California in four thrushes. All four laid an egg in the morning hours of Days 1 through 4. One day following clutch completion (Day 5) is also shown. Black bars indicate when females were tending their nests at night, white bars when they were absent during daytime, hatched bars when they were tending their nests in daytime which includes on-off foraging bouts. Time of thermocouple installation occurred on Day 1 at time X. SR marks time of sunrise, SS time of sunset (PST).

subsequent 170 min, during the coldest part of the day, Tegg dropped to ambient and followed it until she returned to the nest (arrow 2) and began re-warming the eggs. This period of daytime nest attentiveness continued for 366 min whereupon the female departed (arrow 3) for 418 min before coming back on for the night (arrow 4). Thus, there were two daytime periods off the nest, one

TABLE 1. Number and duration of on-off bouts during periods of daytime nest attentiveness by three Hermit Thrushes and one American Robin. Eggs were laid by both species on Days 1 through 4.

	Number of on-off bouts/day		Duration of on-off bouts/day (min)	
Day	Hermit Thrush Mean ± SD	American Robin Total	Hermit Thrush Mean ± SD	American Robin Mean ± SD
1	1[a]	1[a]		
2	3.7 ± 2.9	7	23.2 ± 13.7	65.8 ± 52.3
3	7.3 ± 4.0	12	24.6 ± 22.2	37.7 ± 49.6
4	15.3 ± 1.5	17	10.2 ± 5.4	14.1 ± 5.5
5	21.0 ± 1.7	17	10.5 ± 4.2	13.8 ± 4.6
6	19.7 ± 0.6	16	11.2 ± 8.3	13.5 ± 5.6
7	21.0 ± 1.7	16	11.0 ± 5.3	13.2 ± 2.8

[a] Assumed from observations of American Robins by Schantz (1939).

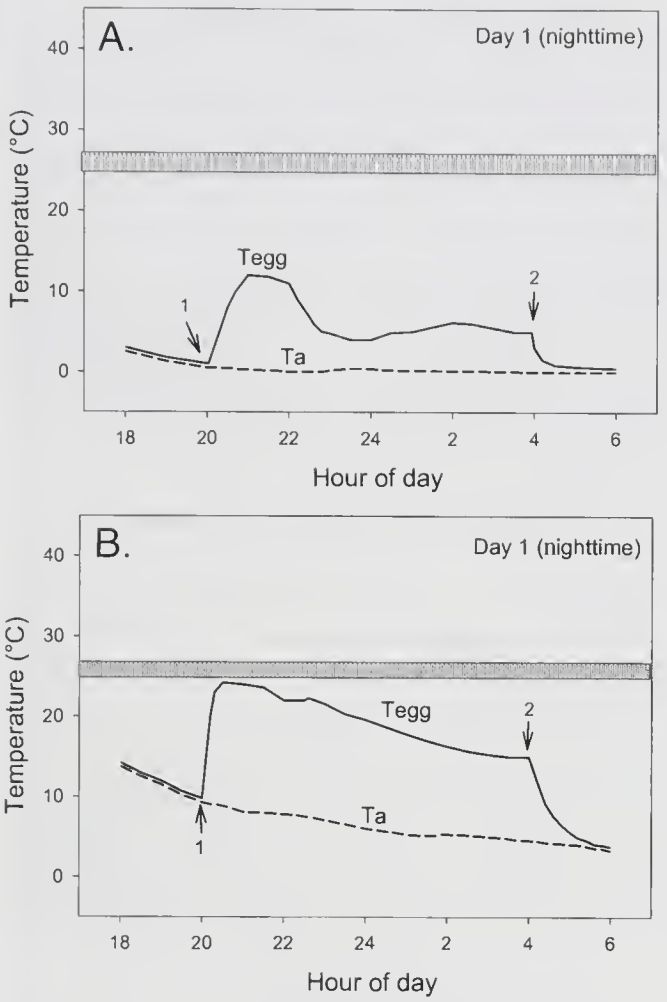

FIG. 2. Egg temperatures (Tegg) in two nests (A = Hermit Thrush; B = American Robin) on the first night following onset of laying (Day 1). Arrow 1 shows when night-time attentiveness began, and arrow 2 when it ended. Concurrent record of air temperatures (Ta) also shown. Shaded horizontal bars indicate physiological zero temperature (PZT).

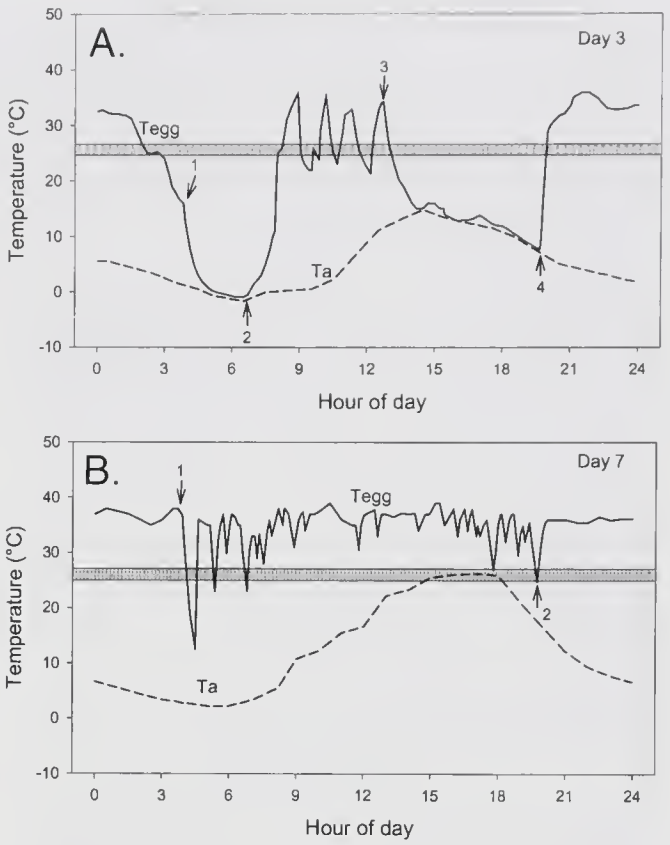

FIG. 3. Tegg and Ta obtained at a Hermit Thrush nest on the day the third egg was laid (A) and 4 days later when regular, full-time incubation was occurring (B). Shaded horizontal bars indicate PZT. See text for explanation of arrows.

in the morning and one in the afternoon (white bars, Fig. 1) when the female was, presumably, mainly engaged in foraging.

An example of this same female's attentiveness pattern is shown 4 days later (Fig. 3B) when she was in full incubation mode. She left the nest in daytime (beginning at arrow 1) only for foraging bouts and remained on the nest at mid-day for extended periods when there was exposure to sun. Eventually, well after sunset, she began the period of night-time attentiveness (arrow 2). Tegg seldom dropped below PZT at this time; embryos were usually sufficiently warm for growth and development to occur.

The percentage of total daytime and nighttime that eggs were heated above PZT increased gradually, but daytime incubation lagged behind that of nighttime (Fig 4). Night-time nest occupancy time was 100% from the first egg onward and daytime occupancy was not (Fig. 1). Incubation onset also occurred more rapidly at night. For example, during the night that Hermit Thrush A was on her first egg it was not warmed sufficiently for development to occur (Fig. 2A). Tegg during the next night, after the second egg had been laid, exceeded PZT 70.8% of the time and on the following night it was 98.7% (Fig. 4A). In contrast, in the daytime hours during which the second egg was laid, PZT was exceeded for only 21 of the 168 min (12.5%) the female was on the nest, or 2.2% of the total daytime period (Fig. 4A). PZT was exceeded in the daytime hours, during which the third egg was laid, for 126 of the 366 min (34.4%) that a female was on the nest (Fig. 3A), or 13.1% of the total daytime period (Fig. 4A). Time that eggs were held above PZT was at or near 100% by the third night for Hermit Thrushes, but daytime heat transfer to eggs was not maximized at 92 to 98% until the day following clutch completion (Fig. 4A, B, C). The American Robin followed a night-time pattern similar to that of Hermit Thrushes, but reached the daytime maximum above PZT (98 to 100%) a day ahead of them (Fig. 4D).

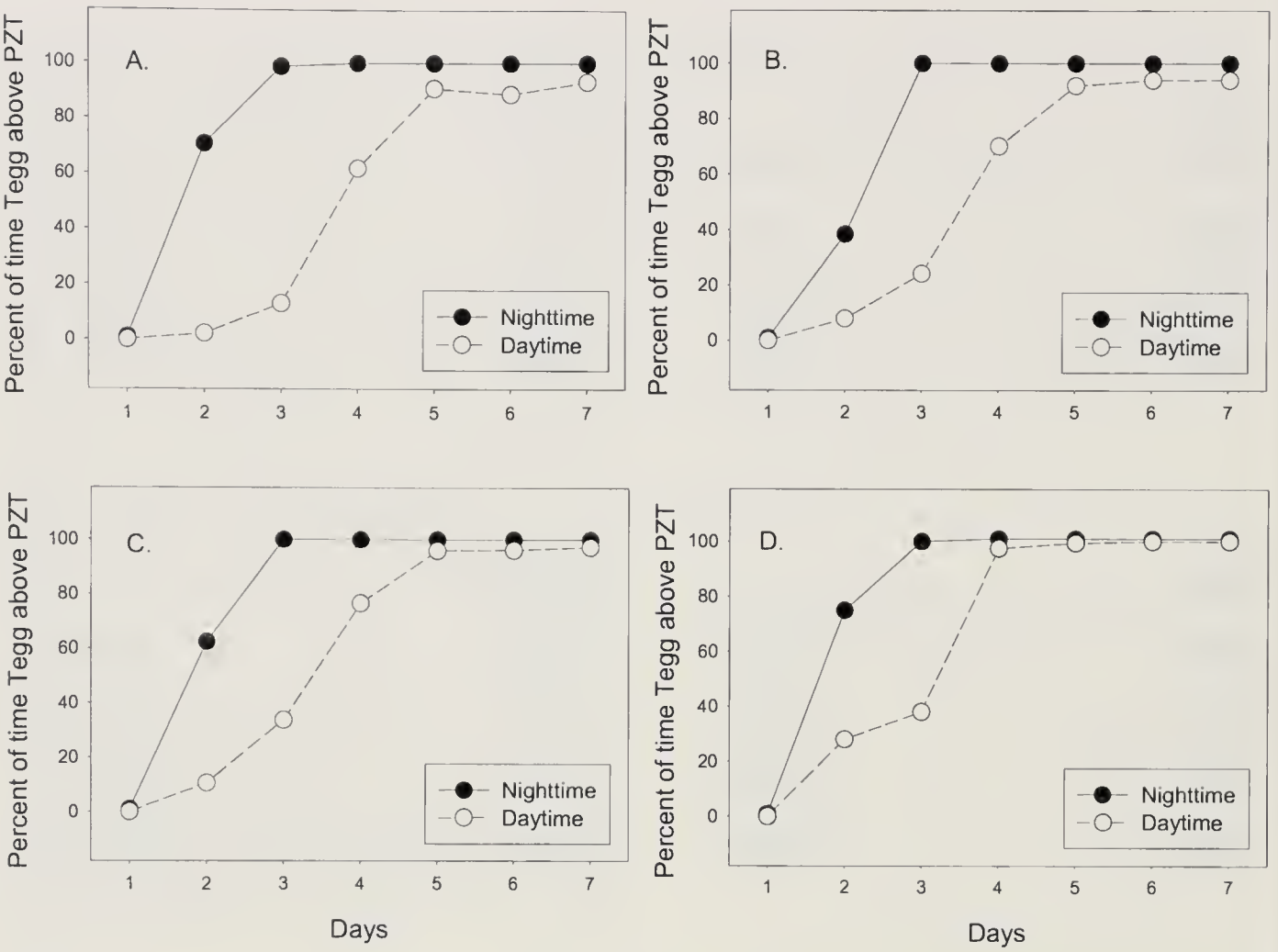

FIG. 4. Percent of time that Tegg was above PZT during nighttime and during daytime for three Hermit Thrushes (A, B, C) and an American Robin (D). Egg laying occurred on Days 1 through 4.

Hermit Thrush females were attentive to their nests about 38% of the time on Day 1 (1 hr of daytime for laying and 8 hrs of nighttime in the first 24 hrs). This increased steadily on each laying day thereafter as more time became devoted to the nest during daylight hours (Fig. 5). In contrast, no incubation occurred on Day 1, but it began to increase thereafter with eggs being heated in the beginning mostly at night (Fig. 4) then more so in daylight, summing eventually to 80% on Day 4 before reaching a sustainable maximum of ~95% on Day 5 (Fig. 5). The American Robin also increased its incubation time with laying, reaching 98% on Day 4.

Frequency of on-off bouts increased during laying until Day 5 for Hermit Thrushes and Day 4 for the American Robin (Table 1). The slightly higher percentage of time eggs were held above PZT by the American Robin occurred because, unlike Hermit Thrushes (Fig. 3B), its eggs seldom cooled to below 28° C when it was off feeding during the cold hours of early morning.

DISCUSSION

Nest-attentive behavior in thrushes differed greatly with time of day. Nocturnal occupancy of nests began with the first egg and was fully

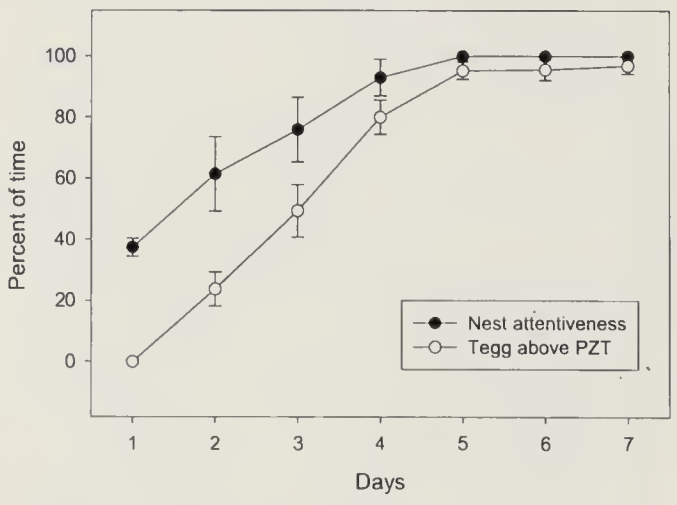

FIG. 5. Percent of time that Hermit Thrush females (n = 3) were tending their nests (filled circles) and warming their eggs above PZT (open circles). Egg laying occurred on Days 1 through 4.

sustained thereafter (Fig. 1). Diurnal attentiveness, in contrast, developed only gradually and was not complete until after the final egg was laid (Fig. 1). Daytime episodes of attentiveness were interrupted by short periods off the nest for foraging (on-off bouts). These increased in frequency and decreased in duration as laying proceeded and became stable at time of clutch completion, a behavioral marker of entry into full-time incubation (Table 1). Aside from those brief forays off the nest there were other, much longer portions of the day, that were presumably devoted mainly to foraging. These lengthy periods of nest neglect occupied more than 90% of daytime hours on the first-egg day (Day 1), decreasing to about 15% on the last-egg day (Day 4) for Hermit Thrushes and to 0% for the American Robin. We hypothesize that females required these long feeding periods to meet the nutritional demands of ovogenesis and that these demands were not trivial. For instance, data on egg weights and body weights of thrushes indicate that clutch mass may exceed one-third of a non-laying female's body mass (Jones and Donovan 1996, Sallabanks and James 1999). Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) on this same study area, had a four-egg clutch mass about equal to 45% of a female's body mass, and resources for ovogenesis were accumulated before and during laying. Body mass increased by about 5% per day in the 3 days prior to first ovulation and decreased only slightly each day thereafter with each new egg. This is about twice the rate of mass gained in females (and males) engaged in autumnal pre-migratory fattening in this same population, indicating that laying females are intensely hyperphagic (Morton 2002).

A trade-off between daytime nest neglect and extended periods for foraging by laying thrushes seems necessary, but what could be the value of their early nocturnal attentiveness? This question was examined for Red-winged Blackbirds (*Agelaius phoeniceus*) by Clotfelter and Yasukawa (1999). They concluded early nest attentiveness did not provide increased egg viability or protection from predators, but may have reduced parasitism by Brown-headed Cowbirds (*Molothrus ater*). Cowbirds were rarely present at Tioga Pass and none of their eggs was detected in 92 Hermit Thrush and 30 American Robin clutches (Morton and Pereyra 2004). Our visits to thrush nests were too infrequent to allow comment on timing of predation (nocturnal or diurnal), but exposure to freezing conditions at night or early morning, as well as severe storms, was known to cause mortality in eggs and nestlings of other species (Morton 2002). Nocturnal attentiveness might preserve egg viability, at least under high altitude conditions. We found on our study area, however, that interspecific variation occurred. Nocturnal attentiveness by four species (Rock Wrens [*Salpinctes obsoletus*], Song Sparrows [*Melospiza melodia*], Hermit Thrushes, and American Robins) began early in the laying sequence (Oppenheimer and Morton 2000, Morton 2002, this study), whereas in two others (Dusky Flycatchers [*Empidonax oberholseri*], White-crowned Sparrows) it was delayed until after the penultimate egg was laid (Zerba and Morton 1983, Morton and Pereyra 1985). Early onset of nocturnal attentiveness occurs in a wide range of passerines, including many cavity nesters (Wang and Weathers 2009), but its adaptive significance seems unresolved.

A key finding of our study was that the pattern of heat transfer to eggs sufficient for embryonic development differed from that of nest attentiveness. For example, all four thrushes began night-time sitting after the first egg (Fig. 1), but none supplied sufficient warmth for incubation to begin until after the second egg (Figs. 2, 4). Hermit Thrushes were attentive for more than half of the daylight hours by Day 3 (Fig. 4A, B, C), but PZT was usually exceeded only briefly during periods that the female was on the nest (Fig. 3A). Mean fraction of daytime where Tegg was sufficiently high for embryonic development on Day 3 was only 23.7 ± 9.5% for Hermit Thrushes and 38.1% for the American Robin (Fig. 4). Females were developing the behavioral rhythm of incubation but full contact of eggs with the incubation patch in daytime was withheld because, during the night-time portion of Day 3, PZT was exceeded by all four thrushes at close to 100% of the time (Fig. 4). This indicates the Day 3 patch was functionally developed but incubation behavior was not with daytime incubation lagging behind nighttime.

Total nest attentiveness behavior and of incubation (daytime plus nighttime) for the 4 days of laying and for 3 days thereafter increased gradually during laying, but with different trajectories (Fig. 5). Hermit Thrushes foraged for at least 2 hrs in early morning before returning to lay their final egg (Fig. 1), and then, immediately thereafter, began full-time incubation. Apparently,

the American Robin dealt more easily with nutritional demands because her prolonged early morning feeding periods ended on Day 3 (Fig. 1D), and incubation behavior was fully developed by Day 4 (Fig. 4D).

Incubation onset in European Starlings (*Sturnus vulgaris*) appeared to be pre-programmed (Meijer 1990), a conclusion supported by our study. For example, day-night timing of heat transfer to eggs during the laying period was much the same for all three Hermit Thrushes and their close relative, the American Robin (Fig. 4). Incubation developed gradually during the laying period in all four birds with full behavioral and physiological capacities converging at the time of clutch completion (Fig. 5). These results agree with those obtained for other species of passerines inhabiting different environments (Wang and Weathers 2009), and with early field observations of Hermit Thrushes (Stanwood 1910) and American Robins (Howell 1942). We suggest this consistency is due to strongly expressed neuroendocrine and endocrine influences (Goldsmith 1982, Sharp 1997, Sharp et al. 1998, Sharp and Blache 2003, Vleck 1998) that have been tuned by natural selection to entrain incubation behaviors that optimize embryonic development and survival.

Results quite different from ours have been published. For example, incubation onset by European Pied Flycatchers (*Ficedula hypoleuca*) occurred at any time within a 4-day span, from the day of clutch completion to 3 days prior (Potti 1998). Even more plasticity was reported in a recent, large study of American Robins wherein females were presumed to begin incubating at any time within a 7-day span, from 4 days after clutch completion to 2 days prior (Rowe and Weatherhead 2009). Accurate information on incubation onset in both of these studies was crucial to the hypotheses presented, yet this key event was defined as the date when eggs first felt warm to the touch. Obviously, according to this criterion, birds could be classified as "incubating" when eggs were under partial incubation, or full-time incubation, or even no incubation if Tegg was below PZT. We hope that more complete information, as provided by egg temperatures, will be obtained before data from studies are incorporated into current paradigms of timing and control of incubation onset.

Studies of incubation have frequently suffered from inconsistencies in terminology and effectiveness of methods, and there has been a failure of investigators to use knowledge about underlying mechanisms. This lack of physiological insight is unfortunate because it can be an impediment to understanding ecological effects (Denny and Helmuth 2009) and even the proximate causation of behavioral phenomena (Drickamer 1998); avian reproduction has model-system potential for collaborations between evolutionary ecologists and endocrinologists (Wingfield et al. 2008). We believe the adaptive value of early incubation onset probably does not lie in hatching asynchrony (Mead and Morton 1985, Morton 2002). It has been shown, for example, that partial incubation before clutch completion can help maintain egg viability (Veiga 1992, Stoleson and Beissinger 1999), and reduce the magnitude of microbial trans-shell infections (Cook et al. 2003).

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FLEXIBILITY IN NEST-SITE CHOICE AND NESTING SUCCESS OF *TURDUS RUFIVENTRIS* (TURDIDAE) IN A MONTANE FOREST IN NORTHWESTERN ARGENTINA

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ABSTRACT.—We studied the consequences of nest-site choice on nesting success under differing disturbance levels for the Rufous-bellied Thrush (*Turdus rufiventris*). We compared nest-site choice and nest success between a disturbed site and an undisturbed site in a montane subtropical forest in northwestern Argentina. We found no overall difference in daily predation rate (DPR) between the disturbed and undisturbed sites. However, DPR of nests on bromeliads was significantly lower at the microhabitat level than on other types of subtrates at the disturbed site. *T. rufiventris* used bromeliads for nesting more often than expected by chance at the disturbed site. DPR did not differ between substrates at the undisturbed site and *T. rufiventris* used all substrates according to their availability. Nests had higher predation at the disturbed site when DPR on non-bromeliad substrates was compared between disturbed and undisturbed sites. Nest fate was independent of nest height. Our results suggest *T. rufiventris*' flexibility in nest-site choice, as reflected by increased use of the safest sites, i.e., bromeliads, in the disturbed site compared to the undisturbed site, may allow this species to survive in an otherwise much riskier habitat. Our results illustrate how microhabitat-scale effects can mediate landscape scale effects.
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Understanding habitat influences on nesting success of birds may be key to their successful conservation, given the sensitivity of this life stage to habitat disturbance (Martin 1992, Easton and Martin 2002). Nest success is influenced by nest-site choice in large part because nest-site characteristics can influence nest predation rates (Martin and Roper 1988, Martin 1993, Holt and Martin 1997, Martin 1998, De Santo et al. 2002, Easton and Martin 2002, Mezquida and Marone 2002, Kellett et al. 2003, Fontaine et al. 2007). Nest predation may be one of the main agents of natural selection influencing evolution of life history traits and nest-site choice (reviewed by Lima 2009, Martin and Briskie 2009). Flexibility in choosing a nest site may allow birds to optimize fitness by exploiting safer substrate types in disturbed conditions, but studies of nesting flexibility and their consequences for nest success are rare.

Nest-site choice, including nesting substrate and nesting height, may be evolutionarily conservative in many species (Martin 1988, Martin and Roper 1988), which may constrain plasticity of choices. Some bird species use the same nest sites in disturbed and undisturbed forest patches, even though this increases predation in disturbed forest patches (Holt and Martin 1997, Easton and Martin 2002). Plastic changes in nest-site selection in response to predation risk have been observed in some species (e.g., Marzluff 1988, Eggers et al. 2006, Peluc et al. 2008). Variation in predation risk is often associated with disturbance of habitats, which also generally reflects differing habitat structure; both differing predation risk and habitat structure could influence nest-site choice (Martin 1992). Few studies have compared nest site choices under differing predation risk or differing habitat structure.

Plasticity of nest-site choice is particularly interesting for tropical and subtropical birds, because they are often thought to have more specialized niches (MacArthur 1972). Consequently, their flexibility of nest-site choice to varying predation risk or habitat structure may be constrained. No study has examined plasticity of nest-site choice by a tropical or subtropical bird. Thus, examination of flexibility of nest-site choice and consequences of that choice on nesting success under differing disturbance levels for tropical or subtropical birds is needed.

Our objective was to test whether nest-site choice and nesting success of the Rufous-bellied Thrush (*Turdus rufiventris*; Turdidae) differed

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between a disturbed site and an undisturbed site in a montane subtropical forest in northwestern Argentina. *Turdus rufiventris* is a common bird that consumes fruits of many species in this environment (Malizia 2001), potentially having an important role in regeneration of native plants. It is widely distributed in central and northern Argentina (Ridgely and Tudor 1989, de la Peña and Rumboll 1998), and is one of the few native forest species that inhabits semi-urban locations (de la Peña and Rumboll 1998, Ferretti et al. 2005). The ability of members of the genus *Turdus*, including *T. rufiventris* (e.g., de la Peña and Rumboll 1998, Ferretti et al. 2005), to live in human-disturbed areas makes them good model species to study how birds adapt to habitat disturbance. Understanding the adaptability of species to disturbance is becoming increasingly important as anthropogenic habitat alterations become increasingly common and intact habitats increasingly rare (Pimm et al. 2001). Examining the effect of habitat characteristics in nest-site choice flexibility and nesting success is important in a threatened but understudied environment such as the subtropics (de la Peña 1979, Mezquida and Marone 2002). We examined nest-site preferences and consequences for nesting success of *T. rufiventris* between undisturbed and disturbed forest sites in northwestern Argentina.

METHODS

The study was conducted between October 1997 and January 1998 at El Rey National Park (hereafter El Rey; 24° 42′ S, 64° 38′ W) in Salta Province, and at Sierra de San Javier Biological Park (hereafter San Javier; 24° 47′ S, 65° 22′ W) in Tucumán Province. Both sites are in northwestern Argentina and are part of the Yungas ecosystem represented by a subtropical montane forest (Brown 1995, Brown et al. 2001). An old cattle farm, El Rey was declared a national park in 1948 and has been preserved intact with no human activity since then. It encompasses 44,162 ha, is 200 km from the nearest city, and no significant logging has been conducted in the area; it represents the undisturbed site. The canopy is dominated by *Cinnamomum porphyrium* (Lauraceae), *Blepharocalix salicifolius* (Myrtaceae), *Cedrella lilloi*, and *C. angustifolia* (Meliaceae). A second stratum is comprised of species typically <20 m high, including *Allophyllus edulis* (Sapindaceae), *Zanthoxylum coco* (Rutaceae), and *Prunus tucumanensis* (Rosaceae) (Blake and Rouges 1997). San Javier was created by the National University of Tucumán in 1973 and covers 14,100 ha; it is 15 km west of the city of San Miguel de Tucumán and 2 km northwest of the city of Yerba Buena. The area has been subject to different land uses including selective logging focused on the most valuable timber species (*Cedrela lilloi*) affecting a large proportion of the sierra, modern agriculture (sugar cane, citrus, horticulture, floriculture), and expanding urbanization (Grau et al. 2008). Trekking and biking trails cross the San Javier site. The secondary forest where we sampled occurs near agricultural and urban sectors (Grau et al. 1997, Aragón and Morales 2003), and represents our disturbed site. Common canopy species at San Javier are *Parapiptadenia exelsa* (Fabaceae), *Cinnamomum porphyrium* (Lauracae), *Juglans australis* (Juglandaceae), and *Myrsine laetevirens* (Myrsinaceae) while the subcanopy is dominated by *Piper tucumanum* (Piperaceae), *Allophylus edulis* (Sapindaceae), and *Psychotria cartagenensis* (Rubiaceae) (Grau et al. in press). The native pioneers *Heliocarpus popayanensis* (Malvaceae), *Tecoma stans* (Bignoniaceae), *Solanum riparium* (Solanaceae), and exotic colonizers including *Morus* spp. (Moraceae), *Ligustrum lucidum* (Oleaceae), and *Citrus* spp. (Rutaceae) (Grau and Aragón 2000) are also common at San Javier. Bromeliads are one of the main groups represented among the abundant epiphytes both at San Javier and at El Rey (Blake and Rouges 1997).

We located nests following Martin and Geupel (1993). This method involves detecting and following birds carrying food or nesting material to the nest, or following female calls. Nest searching was done daily from 0630 to 1245 hrs from October to December. Nests were checked every 2–4 days to record nest stage (e.g., building, incubating, nestlings), number of eggs or nestlings when nests were accessible, nesting substrate, and nest height (Martin and Geupel 1993). The nest was considered failed or fledged if, after three checks, no bird activity was recorded at the nest (the last check had to be at least 30 min), depending on the stage recorded at the last active visit. We were unable to assign the cause of failure of many nests due to inaccessibility, but fledging was confirmed whenever possible by looking for parents with food or fledglings near the nest shortly after the assumed fledge date. We calculated nest success following Mayfield (1961) using the approach outlined by Hensler and

Nichols (1981). We compared daily predation rates between sites and between substrates using a Chi-square test based on program CONTRAST (Hines and Sauer 1989).

The two most common substrates used at San Javier, bromeliads and *Psychotria cartagenensis*, seemed to differ substantially in mean height, and the differences in daily predation rate found between the substrates could be attributed to substrate height and not to type of substrate *per se*. Thus, we tested whether the difference in substrate height was statistically significant using a Mann-Whitney *U*-test, and whether predation was independent of substrate height in San Javier using a Chi-square test.

We measured substrate availability based on the observed substrates used by *T. rufiventris* to examine if nests were randomly placed. We followed the quarter method (Matteuci and Colma 1982), modified to include bromeliad availability. We established two 200 m-long transects at random in the study area. The starting point of the transect was at the end of a random number of steps chosen by a person not familiar with the study site. A second random number indicated the orientation of the transect as measured by a compass. We established four quadrants every 10 m along each of these transects. We projected an imaginary line 17-m high (the maximum nest height recorded during this study) from the center point, and recorded the plant species closest to the imaginary line in each quadrant. We recorded when a bromeliad was the closest substrate, but not the substrate supporting the bromeliad. Only plants with >1.5 cm diameter at breast height (dbh) were recorded because no nest was found on plants with a smaller dbh. At least 160 plants were counted along each transect. We analyzed these data using a *Z*-test for comparing two proportions (Zar 1999) to examine if nest site was chosen according to plant availability.

RESULTS

We found 44 nests of Rufous-bellied Thrushes on 12 different substrates (Fig. 1A) at San Javier of which only 27 had at least one egg laid. Only those 27 nests were used to calculate nest success. All 44 nests at San Javier were included in the substrate use analyses. Sixty-five nests with at least one egg laid were found at El Rey on 19 different substrates (Table 1). These nests were used for estimating nest success and substrate use.

Nests at San Javier were most common on *Psychotria carthagenensis* and bromeliads. However, bromeliads were used in higher proportion than expected according to their availability at San Javier while the other substrates (including *P. carthagenensis*) were used in lower proportion than expected ($Z = 10.8$, df = 2, $P < 0.0001$; Table 2). Substrates at El Rey were used as expected by their availability ($Z = 0.66$, df = 2, $P = 0.26$; Table 2).

Overall daily predation rate (DPR ± SE) at San Javier (0.0684 ± 0.0095, $n = 27$, exposure days = 248.5) did not differ from El Rey (0.0592 ± 0.0089, $n = 65$, exposure days = 709; $X^2 = 0.669$, df = 1, $P = 0.414$). Nest success on *P. carthagenensis*, the most common understory shrub at San Javier, was not different from success on all substrates other than bromeliads ($X^2 = 0.5$, df = 1, $P = 0.48$) and substrates were combined for further analysis. Nests on bromeliads at San Javier were more successful (DPR = 0.0308 ± 0.0175 nests/day, $n = 7$, exposure days = 97.5) than nests on other substrates (DPR = 0.1126 ± 0.0257 nests/day, $n = 20$, exposure days = 151) ($X^2 = 6.92$, df = 1, $P = 0.0085$). Success of nests on bromeliads at El Rey (DPR = 0.0522 ± 0.0207 nests/day, $n = 9$, exposure days = 115) was not significantly different from success on other substrates (DPR = 0.0606 ± 0.0098, $n = 56$, exposure days = 594) ($X^2 = 0.17$, df = 1, $P = 0.68$). We believe that lack of difference between substrates in DPR at El Rey was not affected by low sample size given the significant difference found for San Javier, where sample size was even smaller. Bromeliads were used more often at San Javier than at El Rey, and the high nest success on bromeliads may increase overall nest success at San Javier. Thus, we compared nest success between San Javier and El Rey without considering nests on bromeliads. Non-bromeliad nests experienced higher daily predation rates at San Javier than at El Rey ($X^2 = 4.076$; df = 1; $P = 0.044$).

Nests built on *P. carthagenensis* at San Javier were significantly lower ($\bar{x} = 2.1$ m) than those on bomeliads ($\bar{x} = 8.9$ m) (Mann-Whitney $U = 10$, $P = 0.0004$). However, nest success was independent of nest height ($X^2 = 0.50$, df = 5; $P = 0.48$). Nests occurred between 1 and 17 m above ground with a bimodal distribution (Fig. 1A). Most nests were between 1 and 2 m above the ground with a second peak of nests at 10 m. The two most common substrates mostly explained the distribution of nests at different heights (Fig. 1B).

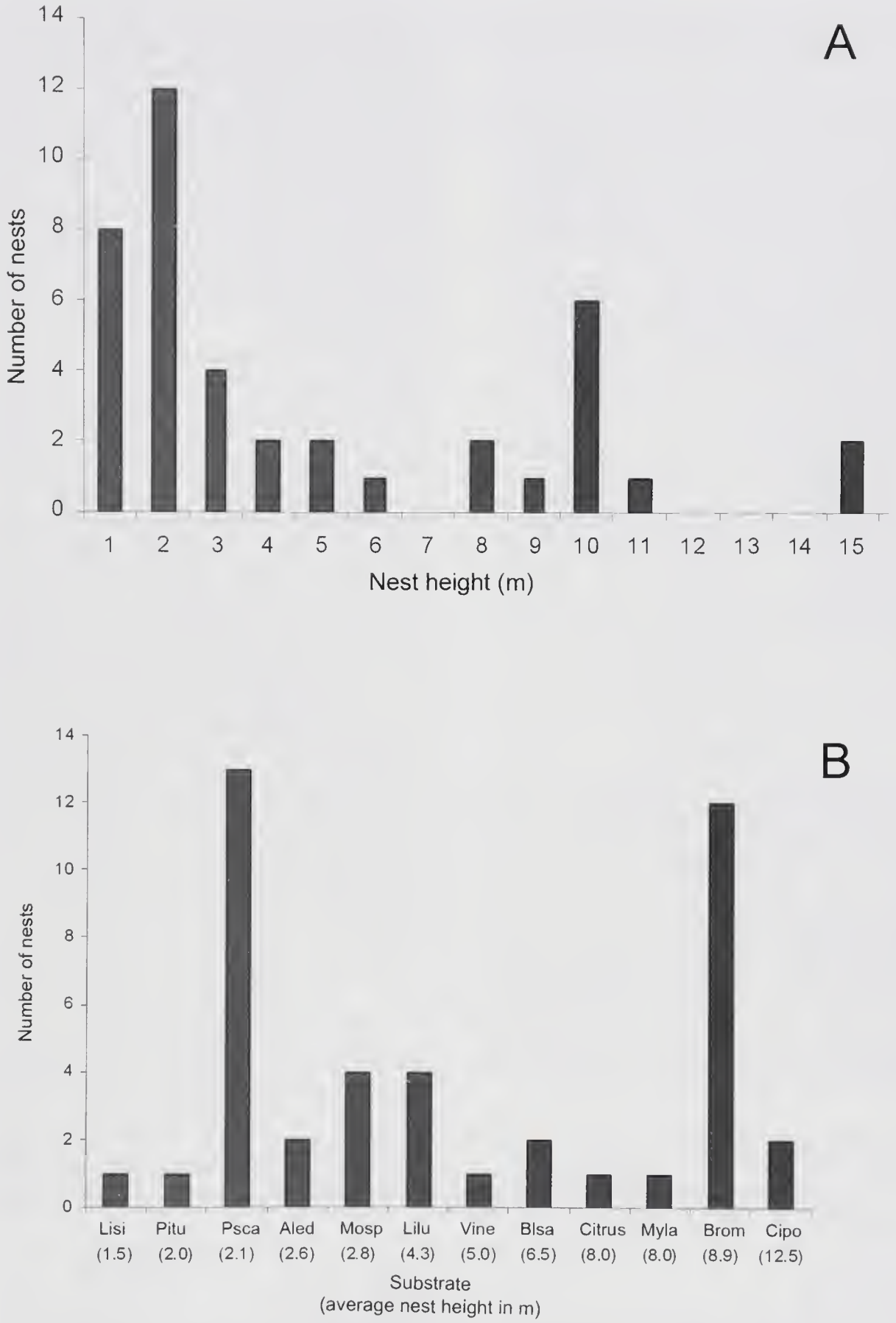

FIG. 1. (A) Distribution of *Turdus rufiventris* nest heights. (B) Number of *Turdus rufiventris* nests found per substrate species (n = 42). Numbers in parentheses show mean height at which nests were built on each substrate. Lisi: *Ligustrum sinense*; Pitu: *Piper tucumanum*; Psca: *Psychotria carthagenensis*; Aled: *Allophylus edulis*; Mosp: *Morus* spp., Lilu: *Ligustrum lucidum*; Vine: unidentified vine; Blsa: *Blepharocalyx salicifolius*; Citrus: *Citrus* spp.; Myla: *Myrsine laetevirens*; Brom: bromeliads; Cipo: *Cinnamomum porphyrium*.

TABLE 1. Substrates used by *Turdus rufiventris* at El Rey National Park, Salta, Argentina.

Substrate species	# Nests	Family
Acacia aroma	3	Fabaceae
A. visco	1	Fabaceae
Allophylus edulis	21	Sapindaceae
Celtis spinosa	1	Celtidaceae
Condalia buxifolia	3	Rhamnaceae
Enterolobium contortisiliquum	1	Fabaceae
Eugenia uniflora	1	Myrtaceae
Gleditsia amorphoides	2	Fabaceae
Nectandra pichurim	1	Lauraceae
Pogonopus tubulosus	1	Rubiaceae
Sambucus peruviana	2	Adoxaceae
Scutia buxifolia	5	Rhamnaceae
Sideroxylon obtusifolium	1	Sapotaceae
Urera caracasana	2	Urticaceae
Vassobia breviflora	1	Solanaceae
Xylosma pubescens	1	Salicaceae
Unidentified bromeliad	9	Bromeliaceae
Unidentified fern	1	
Unidentified moss	2	
Unidentified Myrtaceae	2	Myrtaceae
Unidentified vine	4	
Total	65	

DISCUSSION

The high variability of substrate type and nest height used by Rufous-bellied Thrushes is contrary to that expected if nesting was conserved within a species (Knight and Fitzner 1985; Dhindsa et al. 1988; Martin 1988, 1993; but see Forstmeier and Weiss 2004, Eggers et al. 2006, Peluc et al. 2008). This species nested on at least 12 substrate types, including understory shrubs, bromeliad epiphytes, canopy trees, and exotic as well as native species. *Turdus rufiventris* also placed nests at a wide range of heights from 1.5 to 17 m.

Rufous-bellied Thrushes did not seem to specialize on one substrate type, but were selective of nesting substrate, particularly at the site where microhabitat selectivity was associated with potential fitness benefits. *Turdus rufiventris* favored bromeliads, the substrate associated with highest nest success at San Javier, in accordance with the expectation that birds should maximize nest success (Martin 1998). In contrast, this species was not selective with respect to substrate at El Rey, where predation rates did not differ between nest sites.

Our results on nest-site choice and nest success in relation to disturbance differed depending on the scale at which we analyzed our data. Our results at a large scale did not support the hypothesis that anthropogenic disturbance increases the threat of nest predation (i.e., overall DPR was similar for San Javier vs. El Rey) (Holt and Martin 1997, De Santo et al. 2002, Easton and Martin 2002, Kellett et al. 2003). However, when examined at the microhabitat scale, we found that predation rate was much higher at the disturbed than at the undisturbed site. The higher predation rate at the disturbed site on non-bromeliad nest sites suggests predation rates were higher in the disturbed habitat but birds compensated through nest-site choice. These results confirm the importance of examining ecological patterns at multiple scales (Holling 1992, Levin 1992); if we had ignored microhabitat scale mechanisms, large scale disturbance effects would have been misinterpreted.

What makes bromeliads a safer nesting site at San Javier, and why is this not the case at El Rey? We showed that substrate height is not the determining factor; thus, bromeliads must be influencing other aspects of nest-site structure that affect predation risk. We believe bromeliad

TABLE 2. Nest success and number of nests of *Turdus rufiventris* (Turdidae) on bromeliads and other substrates, and substrate availability at El Rey National Park, Salta, and Sierra de San Javier Biological Park, Tucumán, Argentina.

	El Rey National Park	Sierra de San Javier Biological Park
Overall DPR	0.0592 ± 0.0089	0.0684 ± 0.0095
DPR on bromeliads	0.0522 ± 0.0207	0.0308 ± 0.0175
DPR on other substrates	0.0606 ± 0.0098	0.1126 ± 0.0257
Number of nests on bromeliads (% of total nests)	9 (14%)	7 (26%)
Number of nests on other substrates (% of total nests)	56 (86%)	20 (74%)
Substrate availability		
Bromeliads (%)	7	3
Others (%)	93	97

structure may make nests less visible and less vulnerable to predation by white-eared opossums (*Didelphis albiventer*) and black rats (*Rattus rattus*), which are common around houses in disturbed areas, but not to predation by House Wrens (*Troglodytes aedon*), Plush-crested Jays (*Cyanocorax chrysops*), and brown capuchin monkeys (*Cebus apella*), common nest predators in the undisturbed site (Auer et al. 2007). In addition, the relevant structural feature may be one that only influences predation risk in disturbed areas. Predator communities most likely differ between disturbed and undisturbed sites (Auer et al. 2007; J. P. Jayat, pers. comm.); thus, the relevant structural feature must be one that conceals nests from predators that occur in disturbed sites, either exclusively or at least in higher numbers.

Our results suggest a potential mechanism by which birds could adapt to the negative effects of human disturbance on nest predation risk. *Turdus rufiventris* apparently adjusts its nest-site choices to compensate for elevated predation risk in disturbed habitats. Additional studies of other species that compare both microhabitat choices and microhabitat-predation relationships in disturbed versus undisturbed areas are necessary to establish the generality of this mechanism. Studies of a range of species that vary in adaptability to human disturbance would be particularly helpful. Our ability to make general conclusions from this study is somewhat limited given the inclusion of only one disturbed site and one undisturbed site. Additional studies incorporating more replication would be valuable.

ACKNOWLEDGMENTS

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BREEDING BIOLOGY OF THE TAIWAN BARBET (*MEGALAIMA NUCHALIS*) IN TAIPEI BOTANICAL GARDEN

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ABSTRACT.—We studied the breeding biology of the Taiwan Barbet (*Megalaima nuchalis*) in the Taipei Botanical Garden (TBG) during the 2008 and 2009 breeding seasons. Breeding pairs produced a mean of 1.8 broods per season and had a mean clutch size of 3.0 eggs. The mean incubation period was 13.8 days, and both parents shared incubation. The mean nestling period was ~27.5 days, considerably shorter than that of other Asian barbets. The shorter nestling period may be related to the low fledgling success rate, multiple broods per season, and constant animal matter food in TBG throughout the entire nesting period. Ambient temperature influenced the amount of time spent by adults inside the nest cavity incubating eggs and brooding nestlings. Adult males provided more food to nestlings than adult females, while adult females cleaned the nest more often than males. The overall egg-to-fledgling success rate was low at 32.8%, because of infertile eggs and failure of eggs with embryos to hatch, abandonment, anthropogenic disturbances, predation, weather disturbances, and other unknown factors. *Received 7 January 2010. Accepted 15 April 2010.*

The Asian barbets (Family Megalaimidae) are one of the least studied groups compared to barbets in Africa and Central and South America (Yahya 1988). The Asian barbets belong predominantly to the genus *Megalaima*, which includes 28 species and is centered in Southeast Asia (Short and Horne 2001). Barbets are mostly frugivores and are important pollinators and seed dispersers. Some of the more insectivorous barbets, such as White-cheeked Barbet (*M. viridis*), have a vital role in controlling insect pests in agricultural regions (Yahya 2000). Barbets are primary tree-cavity nesters that excavate their own nesting and roosting holes; thus, losses of dead trunks or branches have detrimental effects on this group (Short and Horne 2001). Gradual shrinkage of forest cover may have a far-reaching effect on barbets as is the case of the Red-crowned Barbet (*M. rafflesii*), which has nearly been eradicated from Thailand because of forest clear-cutting (Wells 1999). Detailed information on the breeding biology of most *Megalaima* spp. is almost non-existent.

The Taiwan Barbet (*M. nuchalis*) is an endemic species restricted to Taiwan, and was a subspecies of the Black-browed Barbet (*M. oorti nuchalis*) until recent genetic comparisons (Feinstein et al. 2008), and morphological and behavioral differences among the subspecies (Collar 2006) gave it full species status. The Taiwan Barbet is commonly distributed throughout Taiwan at low- to mid-elevations. They commonly occur in broadleaf forests in both natural and man-made habitats, including parks, botanical gardens, school yards, and trees along sidewalks. This sexually monomorphic species begins breeding in April and continues into August (Fang 2008); detailed information on its breeding biology and parental roles is extremely limited. Koh and Lu (2009) investigated characteristics of nest trees and nest cavities of Taiwan Barbets in Taipei Botanical Garden (TBG). They discovered the species nested mostly in *Cinnamomum camphora* trees and in dead standing trees or live trees with dead branches. The only other research on this species was of its general biology in Yangmingshan National Park, Taiwan (Ho 1990). Primary cavity nesters such as the Taiwan Barbet can be affected by land management practices, especially in urbanized environments (James and Kannan 2009) where urban trees may be trimmed or completely removed during beautification actions or when the trees pose a safety hazard for pedestrians or vehicles in traffic. The Taiwan Barbet is commonly sold in pet stores and origins of these captures are questionable, and most likely illegal. Our objective is to present information on the breeding biology and behavior of the relatively poorly known Taiwan Barbet. More specifically, we ascertained the length of the incubation and brooding periods, parental roles, and hatching and fledging success rates in Taipei Botanical Garden.

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METHODS

Study Area.—This study occurred in Taipei Botanical Garden (TBG) (25° 01′ 53″ N, 121° 30′ 39″ E) from March to September 2008 and 2009. The botanical garden encompasses 8 ha of urban green space in central Taipei City, Taiwan and has >1,500 living plant species. The monthly temperature ranged from 14.2 to 30.1° C, averaging 22.7° C in 2008 and 2009; monthly precipitation ranged from zero to 1668.5 mm, averaging 209.3 mm (TBG, unpubl. data). This area of high plant diversity and abundance in the heavily urbanized city center provides excellent habitat for urban wildlife, especially avian species. Forty-five avian species have been reported in TBG with 30 resident species and the other escapees, migrants, and transients (Koh 1998). Koh (1998) noted the year-round presence of Taiwan Barbets and categorized their status as resident. The data base from the Wild Bird Society of Ilan in Taiwan (http://wildbird.e-land.gov.tw) indicates Taiwan Barbets were observed almost every month from December 2003 to October 2005, suggesting the presence of a stable population in TBG.

Nest Searching, Observing, and Monitoring.—Searches for paired barbets and their nests were conducted opportunistically on foot within TBG at least once each day from early March to mid-September in 2008 and 2009. Searches were based on visual and auditory cues, and nests were located by following adults. The gender of the adults was ascertained by observing their positions during copulation (male mounting the female from rear) and was identifiable by learning the key features between individuals in the pair. Adults and fledglings were captured in mist nets, measured, and color-banded during the nestling-provisioning stage and after fledging, respectively. The condition and status of nest cavities were inspected using an endoscope. The endoscope is custom made with a pinpoint camera at the end of an extendable pole of up to 6 m in length with a small monitor attached to the camera via extension cables. This equipment allowed us to look inside the nest, and videotape and photograph the nest's current conditions, whether it was a nesting cavity, abandoned, or incomplete. The endoscope also allowed us to identify the dates eggs were laid, clutch size, and stages of nestling development. Breeding behaviors, including cavity excavation, copulation, nestling provisioning, nest cleaning, and time of entrance and exit of parents were observed and recorded using spotting scopes and binoculars from distances that would not disrupt the birds' natural behaviors and actions. Time spent inside the nest cavity during the incubation and nestling periods by adults was defined as incubation time and brooding time, respectively. The brooding time did not include time spent by adults inside the nest provisioning nestlings or nest sanitation.

The incubation period was measured from the day the last egg was laid to the day the first egg hatched and was subdivided into two stages: early (1–6 days after incubation) and late (7–15 days after incubation). The nestling period was from the day the first egg hatched to the day the first nestling fledged. The nestling period was subdivided into two stages: early (1–13 days after hatching) and late (14–27 days after hatching). The nestling period for nest sanitation and nestling provisioning data was subdivided into three stages: early (1–10 days after hatching), middle (11–20 days after hatching), and final (21 days and onward after hatching). Nest sanitation was recorded when adults removed wood chips mixed with fecal matter from the nest cavity, and nestling provisioning was recorded when adults brought food into the nest cavity. Identification of food type was performed to the best ability of the observers. Food types fed to nestlings were categorized as "plant matter", "animal matter", and "unknown". All variables were grouped into temporal periods of 4 hrs each, from 0600 to 1000 (morning), 1000 to 1400 (midday), and 1400 to 1800 hrs (afternoon), to evaluate mean differences of the variables during different periods of the day and between the parents in each time period (Yahya 1988). Success rates were calculated by dividing the number of nestlings or fledglings by the number of eggs or nestlings in the previous life stage, respectively. We removed the nest cavity and retrieved three eggs of ~1 week of age to conduct physical measurements of the eggs from one abandoned and flooded nest. Hourly temperatures were obtained from the weather stations at TBG. The associated temperatures for each incubation and brooding period (hrs and days) were averaged to obtain the mean hourly and daily temperature for each incubation and brooding period.

Statistical Analysis.—Statistical analyses were performed using SPSS for Windows Version 12.0 (SPSS Institute Inc. 2000) and Microsoft Office Excel 2003. Examination of data normality was

TABLE 1. Incubation and brooding periods, and success rates of Taiwan Barbets during 2008–2009 in Taipei Botanical Garden, Taiwan.

	Mean ± SE (*n*)	Range
Number of eggs laid	3.0 ± 0.1 (11)	2.0–4.0
Number of eggs hatched	2.0 ± 0.3 (13)	0.0–4.0
Egg hatching success rate, %	44.0 ± 12.5 (9)	0.0–100.0
Number of nestlings successfully fledged	1.1 ± 0.2 (15)	0.0–3.0
Fledging success rate—relative to number of eggs, %	32.8 ± 9.9 (11)	0.0–100.0
Fledging success rate—relative to number of hatchlings, %	45.4 ± 13.7 (9)	0.0–100.0
Length of incubation period, days	13.8 ± 0.3 (6)	13.0–15.0
Length of nestling period, days	27.5 ± 1.0 (6)	23.0–29.0

conducted using the one-sample Kolmogorov-Smirov test. Means were compared using paired *t*-tests or one-way ANOVA for data with normal distributions. Either Mann-Whitney *U*-tests or Kruskal-Wallis tests were used for data with non-normal distributions. Tukey's HSD tests were used, when appropriate, to examine which means of groups significantly differed from one another. Means ± SE are presented.

RESULTS

The breeding season of Taiwan Barbets began in April when the first observed pair at the study site laid their first egg and ended in August with fledging of the last nestling. We located eight and 20 broods in 2008 and 2009, respectively. Identified pairs in 2008 and 2009 produced a mean of 1.8 broods/pair (range = 1.0–3.0, n = 13) and had a brood success rate of 71.4% (n = 28). The last egg of the season in 2008 was laid on 6 August. However, due to natural weather disturbances, this nest was abandoned and the season terminated on 17 August. The first egg in 2009 was estimated to have been laid on 20 April, and the last nestling fledged on 6 August.

Courtship Behavior and Copulation.—Courtship feeding was observed four times in 2009. Males fed unidentified berries on three separate occasions to females and an unidentified insect on another occasion. Copulation may or may not occur in conjunction with courtship feeding. The male mounted the female in one occasion while still holding three berries in his beak. The female selected one berry after copulation from the male's beak and the male ate the rest. The average copulation attempt was 10.8 ± 4.0 sec (n = 5). An unique behavior observed during the breeding season was the beak-tapping action performed by an adult male at the cavity entrance (n = 4).

Cavity Excavation.—The adult male significantly excavated the nest cavity longer than its partner. Males (n = 4) excavated for 17.6 ± 1.7 min/hr compared to 6.9 ± 0.8 min/hr for females (paired *t*-test, t = 5.447, df = 3, $P < 0.05$). The time required to complete a nesting cavity for one particular pair was 22 days.

Egg Laying and Clutch Size.—Females laid an egg per day (n = 6), and the mean clutch size was 3.0 ± 0.1 (range = 2.0–4.0 eggs, n = 11; Table 1). We opened the nest cavity and measured three eggs from a flooded and abandoned nest cavity. The eggs were white in color and subelliptical-shaped. Mean egg length was 26.9 ± 0.5 mm (range = 26.1–27.7 mm, n = 3) and the mean width was 19.8 ± 0.2 mm (range = 19.4–20.0 mm, n = 3); mean egg weight was 5.4 ± 0.4 g (range = 5.0–5.8 g, n = 2). One other egg was addled when retrieved and weighed 3.0 g.

Incubation Period.—The incubation period began when the last egg of the clutch was laid and lasted 13.8 ± 0.3 days (range = 13.0–15.0 days, n = 6; Table 1). Time spent by adults incubating eggs throughout the incubation period was 34.1 ± 2.3 min/hr (range = 21.6–43.3 min/hr, n = 9). Males and females incubated equally in early and late stages. Incubation occurred most frequently in the early morning and decreased as the day progressed (range = 29.5–47.4 min/hr; Fig. 1). Eggs were most frequently incubated by adults during 0600 to 1000 hrs (ANOVA, F = 3.837, df = 25, $P < 0.05$) when compared to 1000 to 1400 and 1400 to 1800-hr periods (Tukey test, $P < 0.05$). Mean ambient temperature was lowest at 23.4° C during early mornings and increased to 29.5° C from 1300 to 1400 hrs, and then decreased to 27.2° C from 1700 to 1800 hrs (TBG, unpubl. data; Fig. 1). Males incubated longer than females during the 0600 to 1000 and 1400 to 1800-hr periods but the differences were not

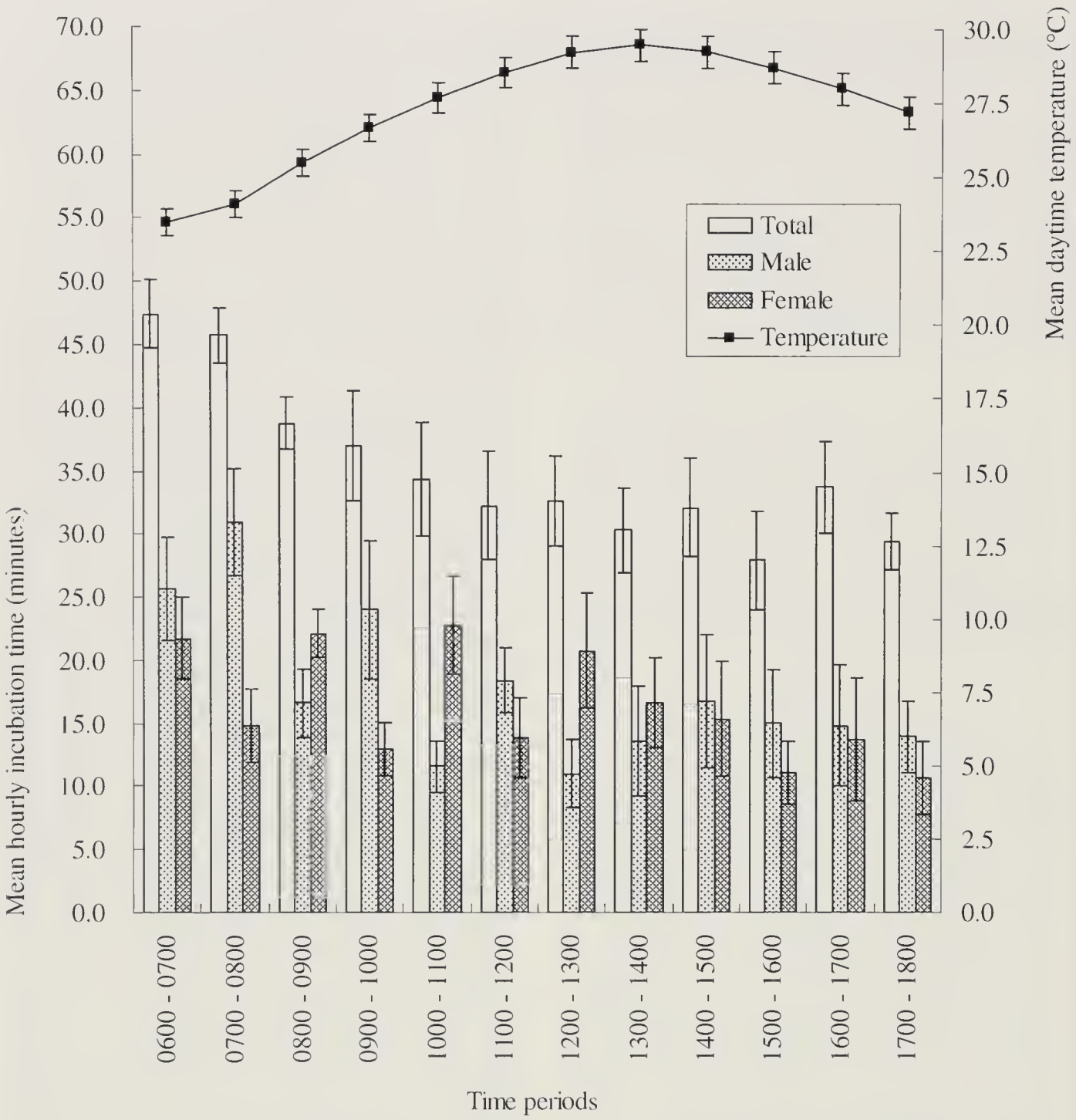

FIG. 1. Hourly incubation time by Taiwan Barbets in different hours of the incubation period, and the mean daytime temperature for each day during 2008–2009 in Taipei Botanical Garden, Taiwan. The mean temperature was calculated by averaging the daytime temperatures of each incubation period. Error bars are ± SE.

significant. Females stayed overnight with the eggs during the 5 days where we continued observation past 1800 hrs (n = 4). The egg hatching success rate was 44.0 ± 12.5% at the end of the incubation period (n = 9; Table 1), and chicks were born naked and with eyes closed.

Nestling Period.—The nestling period of Taiwan Barbets lasted 27.5 ± 1.0 days (range = 23–29 days, n = 6; Table 1). Adults spent 9.0 ± 2.9 min/hr (range = 0.8–21.1 min/hr, n = 8) throughout the nestling period brooding the nestlings, and brooding time in the early stage was significantly longer than in the late stage (independent t-test, t = 4.196, df = 10, P < 0.001). Females spent a longer period of time brooding nestlings than males during the nestling period, but we did not find any significant difference between them. Brooding time by parents was longer in the early morning and decreased at the end of the observation period in

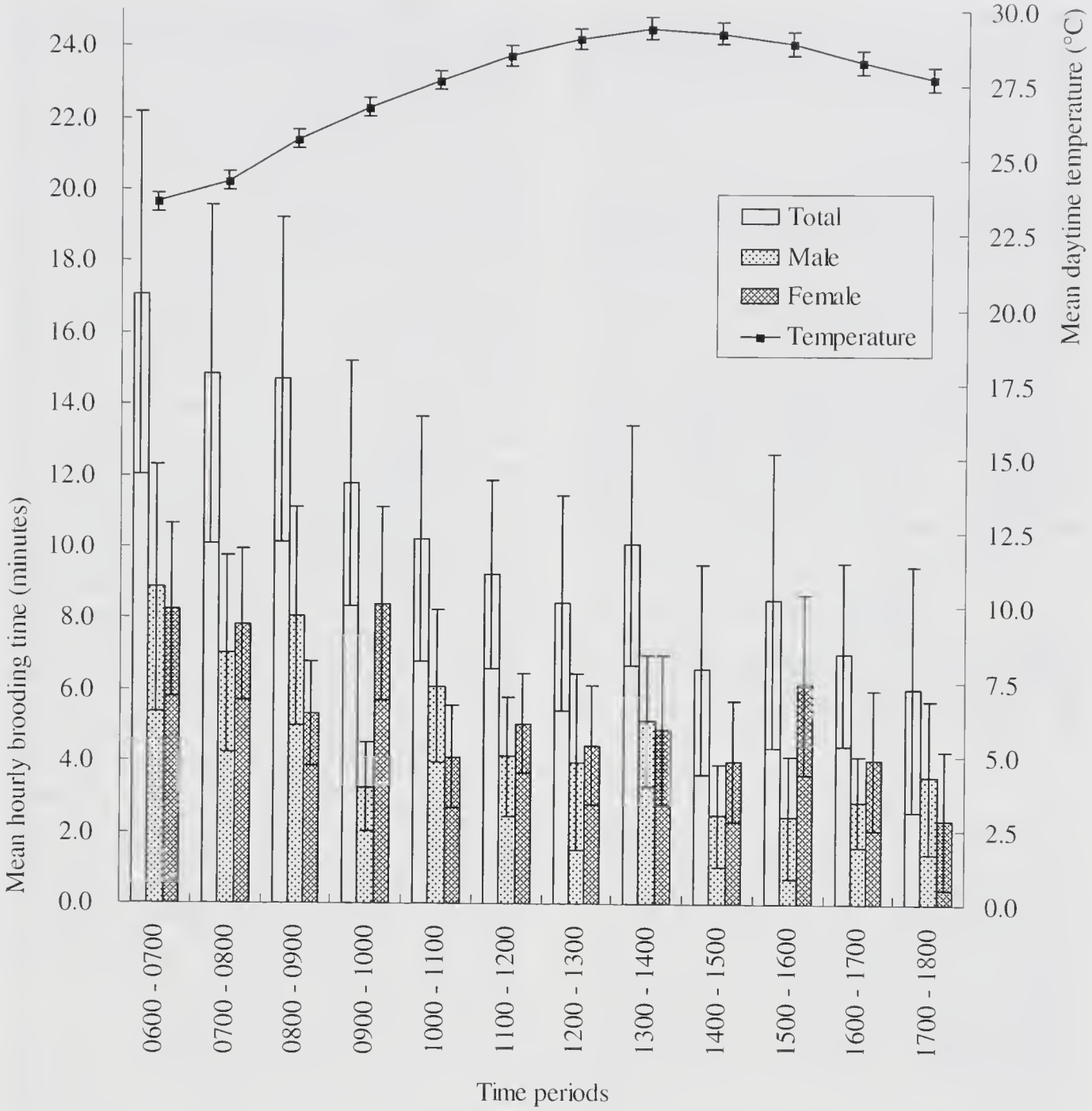

FIG. 2. Hourly brooding time by Taiwan Barbets in diffcrent hours of the nestling period and the mean daytime temperature for cach day during 2008–2009 in Taipei Botanical Garden, Taiwan. The mean temperature was calculated by averaging the daytime temperatures of each brooding period. Error bars are ± SE.

late afternoon (Fig. 2). Temperatures were coolest in the early morning and late afternoon and warmest in mid-day (Fig. 2). Females continued to be the primary parent staying overnight inside the nesting eavity during the nestling period (n = 4) while a male was observed once with the nestlings overnight. Only 45.4 ± 13.7% of the nestlings fledged successfully (n = 9; Table 1).

Nestling Provision, Food Types, and Nest Sanitation.—Frequency of nestling provision and nest cleaning increased as brooding time de-ereased. The overall food provisioning rate was 1.3 ± 0.2 times/hr and increased during the nestling period (range = 0.3–3.0 times/hr, n = 8). On average, males delivered food more frequently but not more significantly than females during the nestling period. The greatest amount of animal matter (27.1%) was fed to nestlings during the middle stage of the nestling period and decreased to 22.3% in the final stage. There were no

differences in food provisioning rates between animal and plant matter during the nestling period. Plant matter consisted entirely of berries from many different plant species, while animal matter consisted of mostly insects, except for four special small vertebrates, one gecko and three lizards. The insects provided to nestlings were: Coleoptera (11.5%), Hemiptera (7.9%), Hymenoptera (1.8%), Mantodea (1.3%), Odonata (<1.0%), Lepidoptera (<1.0%), Orthoptera (<1.0%), and Blattaria (<1.0%); the remainder were insects of unidentified Orders (74.8%) ($n = 8$).

Nest sanitation was a frequent and important task performed throughout the nestling period, averaging 0.9 ± 0.1 times/hr (range = 0.5–1.2 times/hr, $n = 8$) by both parents. Females maintained a higher nest sanitation rate than males throughout the nestling period in all three time periods (paired t-test, $t = -4.206$, df = 7, $P < 0.01$), especially in the early stage (paired t-test, $t = -4.376$, df = 4, $P < 0.05$). Adults cleaned the nest cavity more frequently and significantly during the 0600 to 1000-hr period than in the 1400 to 1800-hr period (Tukey test, $P < 0.05$).

DISCUSSION

The breeding season of Taiwan Barbets began in April, similar to other *Megalaima* spp. that live at similar latitudes. The breeding seasons of some *Megalaima* spp. may start as early as January and end as late as October, but commonly occur from March to July (Short and Horne 2001). Ho (1990) reported the breeding season of Taiwan Barbets in Yangmingshan National Park, Taiwan concluded in late August. The breeding season at TBG also terminated in August. The average breeding season length of Taiwan Barbet in TBG was >3 months in length. We hypothesize that length of the breeding season is affected by weather disturbances, number of broods per pair, length of incubation and nestling periods, and the reproductive condition of adult females after each brood.

Egg Laying and Clutch Size.—The dimensions of Taiwan Barbet eggs are smaller than eggs of *M. oorti nuchalis* documented by Short and Horne (2001). More egg data are needed to provide a more precise range and mean of egg dimensions. The mean clutch of 3.1 eggs was greater than for *M. viridis*, an Asian barbet of similar body size (Yahya 1988). However, *M. viridis* has larger eggs and higher egg hatching success rate than Taiwan Barbets. We hypothesize the Taiwan Barbet's large clutch size helps to compensate for low egg survival.

Incubation Period.—Eggs of the same clutch are laid on consecutive days and hatch on the same day, as observed for *M. viridis* and *M. rubricapilla* (Yahya 1988). Time required for Taiwan Barbet eggs to hatch is ~14 days, within the range of 12 to 15 days for other Asian barbets (Short and Horne 2001). Adults were frequently inside the nest incubating eggs in the early morning and, by late afternoon, their time inside the cavity diminished. This temporal difference is most likely influenced by ambient temperatures. Temperatures were cooler in early morning and late afternoon and warm during the mid-day, which correspond with more and less time by adults incubating the eggs, respectively. *M. viridis* and *M. rubricapilla* parents are also more attentive during cool mornings and rainy days than during the afternoon (Yahya 1988). The effect of ambient temperature fluctuations on behaviors of breeding adults supports the hypothesis that optimal temperature has an important role in affecting the success of breeding pairs (White and Kinney 1974). Males incubated more in morning and afternoon periods than females; we hypothesize males relieve females after their overnight stay inside the cavity and become the primary incubator in the early morning. Males again take on the role of the primary incubator in late afternoon as the female forages and prepares for her nocturnal incubation duty in the evening.

Nestling Period.—The nestling period of ~27.5 days for Taiwan Barbets is short compared to 35–38 days for five small- to large-sized *Megalaima* spp. (Short and Horne 2001). We hypothesize the shorter nestling period may be related to the low fledgling success rate, multiple broods per season, and steady animal matter food provided by the parents throughout the entire nesting period. Martin and Li (1992) commented that length of the nestling periods was inversely related to risks of nest failure and number of broods the parents produced in a breeding season. The fledgling failure rate in our study was relatively high compared to other *Megalaima* spp. (Yahya 1988), and parents did produce multiple broods per breeding season. Taiwan Barbets supplied nestlings with animal matter food during all stages of the nesting period, especially during the middle stage. Adult *M. rubricapilla* and

M. viridis fed their nestlings more plant matter food than animal matter food for the majority of the nesting period (Yahya 1988). We suggest that Taiwan Barbet nestlings are provided with a constant source of animal protein and can develop faster than other *Megalaima* spp.

Provisioning and Nest Sanitation.—Males at our study site have a slightly larger role in provisioning nestlings than females, while females have a larger role in nest sanitation than males throughout the day. Overall, the parents more or less cooperated with each other in nestling provisioning and nest sanitation. A female disappeared during the nestling period on one occasion, leaving the male to do all nest sanitation and nestling provisioning. The three nestlings died in the male's care. This result suggests that fledging success may be greatly influenced by the performance of either parent due to their cooperative roles in nestling provisioning and nest sanitation.

Success and Mortality Rates.—Yahya (1988) reported the egg hatching success for *M. viridis* and *M. rubricapilla* to be 71.1 and 80.0%, respectively, which are higher than that of Taiwan Barbets in our study. Causes for failures of Taiwan Barbets were infertile eggs and failure of eggs with embryos to hatch (40.0%), human influences (25.0%), weather disturbances (15.0%), and unknown egg disappearances (20.0%), possibly a result of nest predation. The fledgling success rate was also lower than for *M. viridis* and *M. rubricapilla* at about 75.7 and 75.0%, respectively (Yahya 1988). The specific causes of nestling mortality are unknown, but 27.2% of the nestlings died inside the nest and were removed from the nest cavity by the parents, and 36.4% of the nestlings starved to death because parents had not returned to the nests. Mortalities of the remaining unfledged nestlings were of unknown disappearances. Potential factors that reduce fledgling success of cavity nesters include nest parasites, nest desertion, starvation of young, predation, and hyperthermia (Ricklefs 1969, Nilsson 1986, LaBranche and Walters 1994). The specific causes that result in low egg hatching and fledgling success rates remain unclear and are a priority for future researchers.

The workload differences between parents and a slightly more important role of females than males during incubation to nestling periods provide a new perspective into the relatively unknown breeding biology of Taiwan Barbets. Low breeding success rates merit attention and protection, especially for threats the species has from city beautification processes and the pet trade industry.

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BREEDING BIOLOGY OF THE GOLDEN-FACED TYRANNULET (*ZIMMERIUS CHRYSOPS*) IN VENEZUELA

WILLIAM GOULDING[1,2,3] AND THOMAS E. MARTIN[1]

ABSTRACT.—We present the first detailed information on the breeding biology of the Golden-faced Tyrannulet (*Zimmerius chrysops*). Information was gathered from 96 nests in Yacambú National Park, Venezuela during the 2002 to 2008 breeding seasons. The enclosed nest was similar to descriptions of nests of other species in the genus. Eggs were laid on alternate days with mean (± SE) clutch size of 1.98 ± 0.02 (n = 45) and fresh weight of 1.616 ± 0.020 g (n = 48). Only the female incubated and the incubation period averaged 16.9 ± 0.3 days (n = 10). Nest attentiveness (% time on the nest) averaged 66.0 ± 1.6% (n = 40) and increased from early to mid- and late-incubation. Incubation behavior yielded an average 24-hr egg temperature of 34.88 ± 0.45° C (n = 7 nests, 43 days). The nestling growth rate constant for body mass (k = 0.285 ± 0.011) was slow even for tropical tyrannids. The nestling period for nests where exact hatch and fledging days were observed ranged from 17 to 19 days with an average of 18.0 ± 0. 2 days (n = 9). Both females and males fed nestlings at a rate that increased over the nestling period with a mean of 4.41 ± 0.65 trips/hr (n = 10) during days 1 and 2 after hatching, and 14.93 ± 2.36 trips/hr (n = 6) at pin-break (days 10–11). Daily predation rates were similar in egg-laying (0.052 ± 0.025; n = 76.5 exposure days) and incubation periods (0.068 ± 0.010; n = 575.5 exposure days), but were lower during the nestling period (0.039 ± 0.010; n = 377.0 exposure days). The total daily predation rate (0.057 ± 0.007; n = 989.0 exposure days) indicated only 12% of nests were successful. These breeding biology parameters for *Z. chrysops* differ substantially from other tyrant-flycatchers and temperate species, further highlighting the diversity within the Tyrannidae.
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The Golden-faced Tyrannulet (*Zimmerius chrysops*) is a member of the complex and large New World Family Tyrannidae. Tyrannids are diverse in behavior and occupy a broad range of habitats and niches, reaching their greatest diversity in the Neotropics (Ridgely and Tudor 1994, Hilty 2003, Fitzpatrick 2004), where they comprise >20% of passerine species (McGowan 2004). General trends in avian life histories cannot be clarified without studies of tropical species to compensate for the historical bias toward temperate species (Martin 1996, 2004; Stutchbury and Morton 2001). The paucity of information on tropical bird species is particularly evident for tyrannids. Information on the breeding biology of most tropical tyrannids is sparse despite their prominence in the neotropical avifauna, and diversity of form and function.

Zimmerius chrysops is an example of the sparse information on tropical tyrannids. Published breeding biology information on *Z. chrysops* is little more than a description of the enclosed, dome-shaped nest with a side entrance, and observed breeding dates (Hilty and Brown 1986, Best et al. 1996). Yet, it is broadly distributed with a range that extends from Peru, north through the Andes to Colombia and Venezuela, and occurs from ~300 to 2,400 m asl (Hilty and Brown 1986, Ridgely and Tudor 1994, Hilty 2003). The species is associated with the middle to upper forest layers, secondary growth, forest edges, as well as with plantation and garden habitats (Fjeldså and Krabbe 1990). Our objectives are to: (1) present detailed reproductive biology information for *Z. chrysops*, and (2) compare this information with available temperate and tropical avian life history information.

METHODS

We studied Golden-faced Tyrannulets during the March–June breeding seasons in 2002–2008 in Yacambú National Park, Lara State, Venezuela (09° 42′ N, 69° 42′ W). Yacambú contains premontane and montane cloud forest of the northern Andes and encompasses a gradient from 500 to >2,300 m asl (Fierro-Calderón and Martin 2007). Peak precipitation in Yacambú occurs from late April through July (Fierro-Calderón and Martin 2007) with clouds and rain usually enveloping habitats after the morning period, producing cool wet conditions. We worked with equal field effort in the same areas across years in a 1,350 to 2,000 m asl research area.

Nests were located primarily by observing parental behavior, but also by systematic searching. Dimensions of newly constructed nests were measured before use and weather affected their

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shape. Eggs were described following Preston (1953) as clarified by Palmer (1962). Eggs were weighed for fresh egg mass between days 0 and 3 of incubation, and opportunistically later. The incubation period was defined as the period between the last egg laid (day 0) and the last chick hatched (Nice 1954, Martin 2002). Nestling period was defined as the number of days between the last egg hatching and the last chick leaving the nest.

Video cameras were placed at a discreet distance (≥5 m) from the nest and camouflaged with vegetation to minimize any influence on parental behavior. Nests were filmed from 30 min after sunrise for 6 to 8 hrs (Martin and Ghalambor 1999, Martin 2002). Filming occurred on days 2–3 in early incubation, during the middle of the incubation period, and ~2–3 days before expected hatch day (early, middle, and late incubation). Nests found after laying were filmed opportunistically on other days (Martin 2002). Nest attentiveness at individual nests was measured as the percent time females were on the nest based on the number of minutes spent incubating divided by the total number of minutes a nest was filmed (Martin 2002).

Incubating egg temperatures (° C) were measured by inserting a thermistor into the egg center through a small opening in the shell that was sealed with adhesive (Weathers and Sullivan 1989, Martin et al. 2007). HOBO Stowaway XTI dataloggers (Onset Corp., Bourne, MA, USA) were connected to the thermistor by discreetly inserting a fine wire through the nest-wall. Thermistors were inserted within the first 2 days of incubation and dataloggers recorded temperatures in 12–24 sec intervals for 5–7 days per nest following Martin et al. (2007).

Nests were videotaped during the early nestling period (days 1–3), during pin-break when flight feathers broke their sheaths (days 10–11), and the late nestling period preceding expected fledging (day 15 and above). Nests were opportunistically filmed on other days. Videotapes were analyzed for parental brooding attentiveness (%) based on the number of minutes brooding divided by the total number of minutes a nest was filmed, as well as the number of provisioning trips/hr (Martin and Ghalambor 1999, Martin et al. 2000b). Analysis of variance (ANOVA) was used to test for changes in incubation and nestling attentiveness between stages. Changes in brooding and provisioning rates with nestling age were analyzed using correlation coefficients (r).

Chicks were measured every second day (from day located) at the same time of day and at pin-break. Standard measurements taken were mass, tarsal length, wing chord, and primary feather pin measurements. These data were used to calculate the growth rate constant (k) following Ricklefs (1967) and Remeš and Martin (2002). Overall nesting success and predation rates for egg-laying, incubation, and nestling periods were calculated using the Mayfield method (Mayfield 1961, 1975; Hensler and Nichols 1981; Johnson 2007). Chi-square tests of independence (X^2) were used to test for differences in daily predation rates among nest stages (egg laying, incubation, and nestling periods).

Egg and nestling masses were measured using an ACCULAB (Elk Grove, IL, USA) portable electronic scale with a precision of 0.001 g; all measurements were taken using Mitutoyo Digital Calipers (Kingsport, TN, USA) with a precision of 0.01 mm. SPSS Version 15.0 (2006) was used for statistical tests and means are given ± one standard error (SE).

RESULTS

Breeding Habitat.—Golden-faced Tyrannulets nested most commonly near 1,400 m asl and were not encountered above 1,500 m asl. This altitudinal zone contained primary and secondary growth premontane and montane cloud forest with patches of regenerating coffee (*Coffea arabica*) plantations. Active nesting pairs were encountered near forest edges including roads, forest trails, water bodies, and areas of historical disturbance inside the forest boundary. Areas where nests were found contained suitable resources for nest construction (moss and lichen) on tree trunks.

Nest Construction and Sites.—Pairs were observed exploring potentially suitable nest locations together prior to the nest-building process. Only one of the pair, presumably the female, constructed the nest (n = 88 nest-building observations), but the mate generally accompanied the nest-building individual. Nests were typically constructed in a ball of moss on the side of a tree, under a branch, or in an epiphyte (Fig. 1). Two distinct building approaches were observed for nest construction. The first and more common approach involved building into an existing lump of moss or lichen. The second involved building the globular nest onto a bare trunk surface. In the first approach, when a suitable portion of moss or lichen was identified,

FIG. 1. Typical nest (with eggs and nestling) of the Golden-faced Tyrannulet with incubating female (Photographs by W. Goulding).

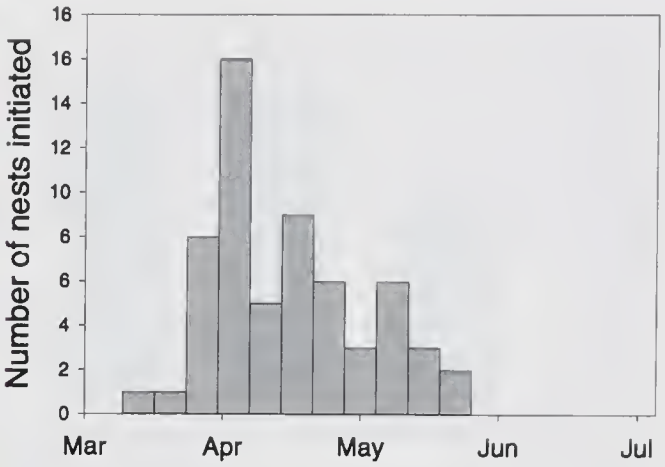

FIG. 2. Seasonal distribution of nest initiation (date the first egg is laid in a nest) for the Golden-faced Tyrannulet at weekly (7 day) intervals.

the adult would open a cavity first with the beak and head and, when at the mid-body section, would use its wings to thrust apart the moss and widen a cavity. The adult would collect materials to create the inside of the nest once a cavity was established. The adult used more of the other nesting materials for construction inside with the moss *in situ*. However, in the second approach where the nest was created on a relatively bare surface, initial construction involved slinging the nest material with spider webs from a point on the bark or from a small piece of moss or lichen. Females were observed repeatedly descending to the ground to scour exposed banks and road cuttings for rootlets and spider webs during construction (e.g., 6 visits in 10 min to the same location on a bank). They also loudly called from beside the nest after building visits with the nearby male usually responding. Females were observed re-using nesting material from previous unsuccessful nests, particularly the lining, but new material was often used. The small size of the nest often resulted in destruction of the nest during predation events.

The mean height of nests above ground was 5.43 ± 0.42 m (n = 55). The external measurements were 116.14 ± 4.27 mm (n = 10) in height by 70.83 ± 2.50 mm (n = 6) in width. Nest cups had an external depth of 48.25 ± 2.87 mm (n = 10) with internal depth and internal diameter being 32.85 ± 2.55 mm (n = 10) and 40.57 ± 2.71 mm (n = 7), respectively. Analysis of 11 nests showed an outer supporting structure of moss into which spider webs, black rootlets, lichen, and spider egg-casings of varying proportions were inserted with internal layers of finer dark rootlets. The final internal layer was a golden lining of soft, comose seed-arils fitting descriptions of liana seeds in the genus *Odontadenia* (Apocynaceae) (Orlando Vargas Ramirez, pers. comm.). The golden lining was characteristic of all *Z. chrysops* nests that we observed.

The earliest nest was initiated (i.e., first egg laid) on 13 March and the latest on 15 May with a mean initiation date of 11 April ± 2.2 days (n = 61) across years (Fig. 2). Nest-building activity began in February. Two nests that fledged chicks in early May 2006 were re-used in February 2007 with new material added.

Eggs and Clutch Size.—Eggs were elliptical in shape and cream-white with liver-brown spots and markings mostly concentrated in a ring toward the obtuse end (Fig. 1). Eggs were 17.17 ± 0.25 mm in length by 13.42 ± 0.11 mm in width (n = 11). Eggs weighed between 1.286 and 1.861 g with a mean mass of 1.616 ± 0.020 g (n = 48). Fresh egg weight represented 18% of mean adult body mass of 9.0 ± 0.2 g (n = 25).

Clutch size was usually two with only one of 45 nests found prior to incubation having a single egg, yielding a mean clutch size of 1.98 ± 0.02 eggs (n = 45). The mean number of days observed between nest completion and laying of

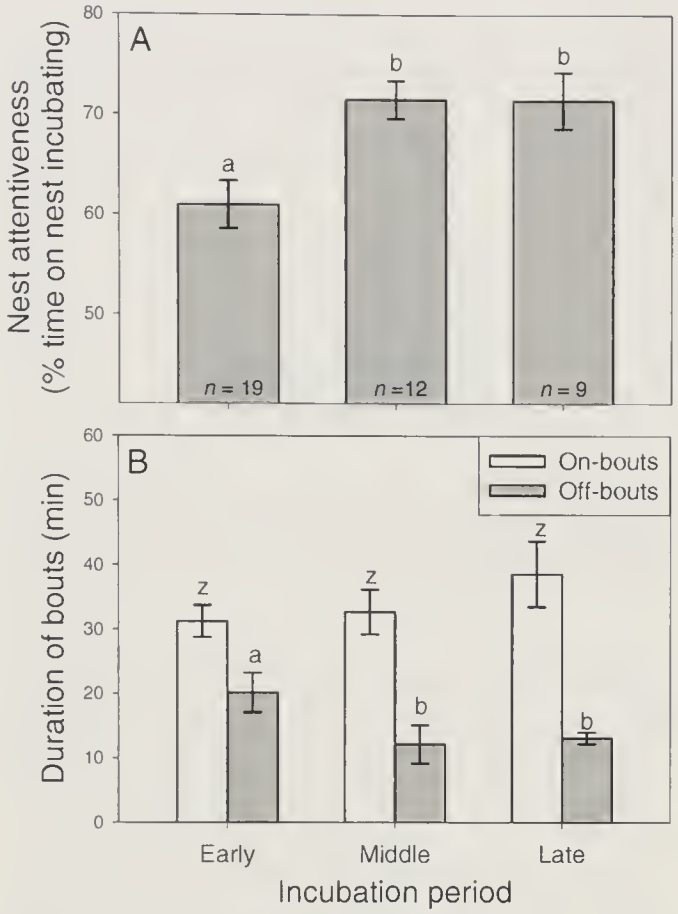

FIG. 3. Average (A) nest attentiveness, and (B) on- and off-bout durations across three periods of incubation: early (days 1–5), middle (days 6–11), and late (days 12–18). Sample sizes reflect numbers of nests.

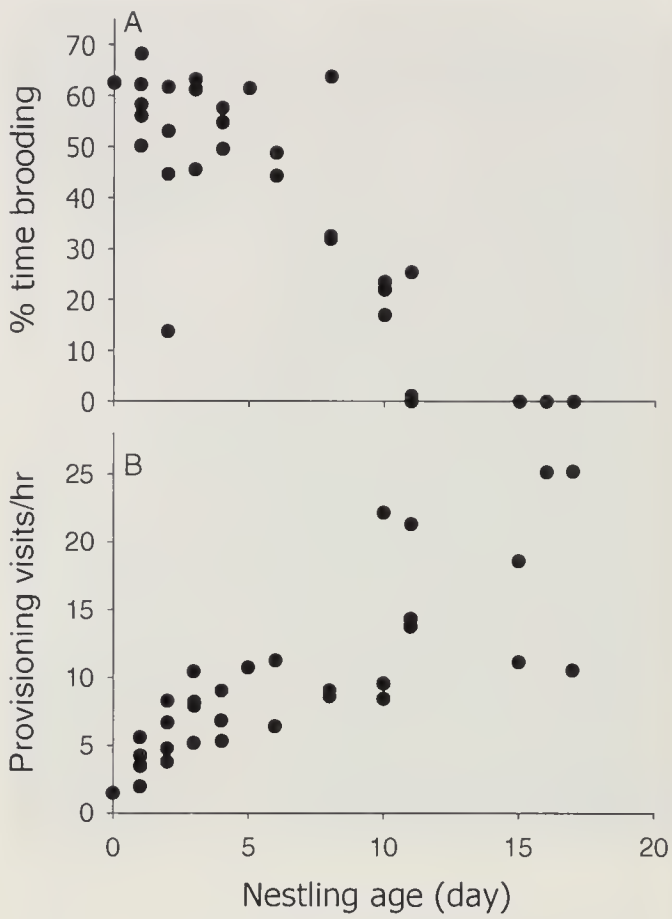

FIG. 4. The change with nestling age in (A) female brooding behavior (% time spent brooding) and (B) rates that parents visit the nest to provision nestlings.

the first egg was 4.71 ± 0.47 (n = 7). Eggs were laid in the morning on alternate days.

Incubation.—Females incubated the eggs without help from males. Males were rarely observed visiting nests during incubation, and did so at only two of 40 nests with video observations of 6–8 hrs each, yielding an average of 0.01 ± 0.01 visits/hr (n = 40).

Females were not observed incubating prior to laying the last egg and eggs hatched synchronously. Nest attentiveness averaged 66.0 ± 1.6% (n = 40) and was lower (ANOVA, $F_{2,37}$ = 6.8, P = 0.003) in early incubation compared with middle and late incubation periods (Fig. 3A). Incubation on-bouts averaged 33.35 ± 1.94 min (n = 40) and did not change over the incubation period (ANOVA, $F_{2,37}$ = 1.1, P = 0.3; Fig. 3B). Length of off-bouts averaged 16.19 ± 1.59 min (n = 40) and decreased from early to later incubation stages (ANOVA, $F_{2,37}$ = 3.2, P = 0.055; Fig. 3B). Incubation behavior yielded an average 24-hr egg temperature of 34.88 ± 0.45° C (n = 7 nests, 43 days of sampling). The incubation period was 16.9 ± 0.3 days (n = 10) for nests found prior to beginning of incubation and where exact hatch was observed.

Nestling Period.—Both adults were observed provisioning chicks and the male was also observed passing food to the female when she was brooding. Adults regularly fed the nestlings fruit that appeared to be mistletoe berries (possibly *Antidaphne viscoidea* or *Phoradendron* spp.), which were regularly found stuck near the beak of chicks. Females regularly regurgitated seeds when incubating and brooding, taking care to eject them outside the nest. The percentage of time females brooded decreased through the nestling period (r = −0.86, P < 0.001), and stopped after the eighth primary pin feather broke its sheath on days 10–11 (Fig. 4A). Provisioning rates increased over the nestling period (r = 0.80, P < 0.001, Fig. 4B). Parents visited the nest an average of 4.41 ± 0.65 trips/hr (n = 10) during days 1 and 2 after hatching, and 14.93 ± 2.36 trips/hr (n = 6) at pin-break.

Chicks had gray down distributed lightly over the head and body, and orange skin and beak at hatching (Fig. 1). The nestling period for nests where exact hatch and fledging days were

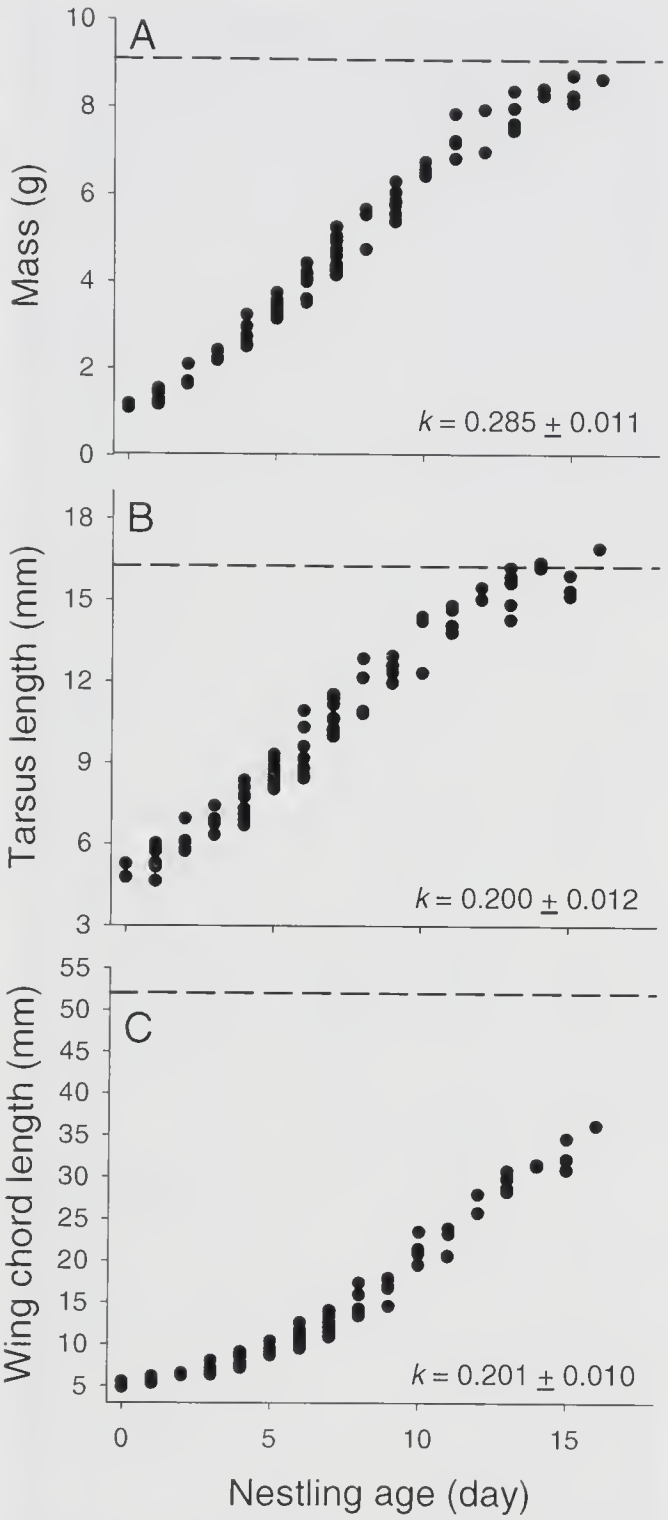

FIG. 5. Relationships of (A) mass, (B) tarsus length, and (C) wing chord length plotted against age for Golden-faced Tyrannulets and their estimated growth rate constants (k). The dashed lines represent mean adult sizes.

observed ranged from 17 to 19 days with an average of 18.0 ± 0.2 days (n = 9). Nestling mass on days 10 and 11 (i.e., pin-break) was 6.966 ± 0.152 g (n = 9). The growth rate constant (k) for body mass was low (Fig. 5A) and nestlings were close to mean adult weight of 9.0 ± 0.2 g (n = 25) at fledging (Fig. 5A). Growth rate based on tarsus length was slower at k = 0.200 ± 0.012 and tarsus size was essentially the same length as adults at 16.26 ± 0.17 mm (n = 22) at fledging (Fig. 5B). Growth rate based on wing chord was k = 0.201 ± 0.010, but wing chord at fledging was less than adult size (Fig. 5C) of 52.03 ± 0.62 mm (n = 20).

Nesting Success and Predation.—Predation accounted for 91.6% of failures with remaining failures attributed to nests falling, abandonment, and poor nest condition that allowed chicks to fall out (re-used nest). Birds seemed to be a main predator of nests with punctured egg remains at times found near the nest. Nest predation often coincided with presence of army ants (*Labidus praedator*) and large mixed-bird flocks feeding near the nest. One nest was also filmed being predated by a capuchin monkey (*Cebus olivaceus*). Snakes were not recorded in video observations and rarely observed at this elevation in Yacambú across all years (TEM, pers. obs.).

The total daily predation rate was 0.057 ± 0.007 (n = 989 exposure days) with a total daily mortality rate of 0.064 ± 0.008. An estimated 12% of nests were successful based on a total nesting period of 37 days. The daily nest predation rate during egg-laying (0.052 ± 0.025; n = 76.5 exposure days) did not differ (X^2 = 0.4, P = 0.6) from the incubation period (0.068 ± 0.010; n = 575.5 exposure days). However, the daily predation rate during the nestling period (0.039 ± 0.010; n = 377 exposure days) was lower (X^2 = 4.2, P = 0.029) than during incubation.

DISCUSSION

Golden-faced Tyrannulets in Yacambú National Park exhibited breeding biology parameters different from most typical tyrannids (Fitzpatrick 2004). The nest appears globular, as also described for congeners (e.g., *Z. acer* [Beebe et al. 1917], *Z. improbus* [Hilty 2003], and *Z. vilissimus* [Skutch 1960]), but varied in appearance depending on location of attachment and amount of exposed nest. Nests of *Z. chrysops*, compared with congeners, were slightly larger than those of *Z. vilissimus* (Skutch 1960), but had a shallower nest-cup than observed for *Z. acer* (Beebe et al. 1917; this was a single observation). Nest construction and materials were virtually the same as those observed for *Z. vilissimus*, including the soft seed-aril lining (Skutch 1960), and similar to *Z. acer* (Beebe et al. 1917). The use of epiphytic

plant resources for nesting by neotropical birds is well recognised (Nadkarni and Matelson 1989, Fierro-Calderón and Martin 2007).

Golden-faced Tyrannulets show flexibility in nesting height with 71% of nests in Yacambú below the 8–12 m height range observed in Colombia (Hilty and Brown 1986), and a nest recorded ~45 m above ground in an emergent *Ceiba* tree in Ecuador (Cisneros-Heredia 2006). Our observations do not seem to reflect biases towards finding low nests because we found the majority of nests through parental behavior. We found nests to the tops of canopies by watching parental behavior. The lower height of nests at our site might reflect the lower stature of the disturbed forest areas and edges in which the species occurred at our site. Differences between nesting height in disturbed or regrowth areas and primary forest have been observed in other tyrannids (e.g., *Z. vilissimus* [Skutch 1960] and *Todirostrum chrysocrotaphum* [Hilty and Brown 1986]), indicating structural differences in habitat influence nest height variation.

Nest architecture seems to be an evolutionarily conservative character that has been used to indicate phylogenetic relationships (Mobley and Prum 1995, Sheldon and Winkler 1999, Zyskowski and Prum 1999). Enclosed nests are thought to be a derived character from the more common open nests reported for the majority of tyrannids (Collias and Collias 1984, Fitzpatrick 2004). It is also thought to be a character that evolved independently in different tyrannid subfamilies (Fitzpatrick 2004). The sparse available information on nests of species of *Zimmerius* indicates only subtle differences between congeners. However, nests of the majority of species in the genus have yet to be investigated. Nest similarity may support a close relationship between *Camptostoma* (Haverschmidt 1954) and *Zimmerius* (unless evolved independently; Lanyon 1988). These two genera, together with the closely related *Phyllomyias virescens* and others in that genus that may be discovered to have enclosed nests (Fitzpatrick 2004, Ohlson et al. 2008, Rheindt et al. 2008), represent the only enclosed nest-builders in the elaeniine clade proposed by Ohlson et al. (2008). Despite differences in external materials, they have similarly attached and shaped immobile nests lined with 'plant wool' (not feathers) with a simple side-opening near the top (Beebe et al. 1917, Haverschmidt 1954, Skutch 1960, this study).

The observed peak of breeding activity of *Z. chrysops* is just prior to and overlapping the peak precipitation period from late April through July in Yacambú (Fierro-Calderón and Martin 2007). This is a pattern in avian breeding biology observed at other neotropical sites (Skutch 1950, 1960; Marchant 1959; Best et al. 1996; Medeiros and Marini 2007), including some species in lowland habitats in Venezuela (Cruz and Andrews 1989). This peak fits within the general breeding period of January to June described for tyrant-flycatchers north of Peru (Fitzpatrick 2004). The season is relatively short compared with other passerine species in this area (e.g., Biancucci and Martin 2008, Niklison et al. 2008, Cox and Martin 2009). Skutch (1950) found from his observations in Central America that, in general, avian populations at higher altitudes exhibited a more marked and narrow breeding season than in lowlands. *Z. chrysops* is thought to breed in Colombia from April until November at the lower elevation of 1,000 m asl (Hilty and Brown 1986). A record in February from Loja Province in Ecuador also reports nesting activity by the species at a similar altitude to Yacambú sites (Best et al. 1996). The short season and absence of any observations of birds re-nesting in the same season after a successful breeding attempt indicates this species is single-brooded, typical of tyrannids (Fitzpatrick 2004).

Eggs of *Z. chrysops* conform to the typical egg coloration observed in most tyrannids (Von Ihering 1904, Skutch 1960, Wetmore 1972). They are slightly larger than an egg of *Z. acer* measured by Beebe et al. (1917) and slightly shorter and wider than eggs of *Z. vilissimus* observed by Skutch (1960). The clutch size of two is on the lower edge of the range of 2–6 observed in the family and the 2–4 of most tropical tyrannids (Fitzpatrick 2004).

The 17-day incubation period is long relative to the range of 12 to 16 days known for most temperate and tropical tyrannids, and approaches a few unusual tropical species that have suspended pendulant nests and long incubation periods (Fitzpatrick 2004). However, the incubation period was near the average for 33 other non-tyrannid species studied in Yacambú National Park (Martin and Schwabl 2008). The 18-day nestling period also is in the upper range for tyrannids, which is from 12 to 24 days with most being 14 to 17 days (Fitzpatrick 2004). Our observations support that mistletoe fruit in the

area (e.g., *Antidaphne viscoidea*; Restrepo et al. 2002, Kelly et al. 2004) comprise an important portion of the diet of nestlings, as with *Z. vilissimus* (Skutch 1960), and not only for adults for which this has already been observed with others in the genus (Fjeldså and Krabbe 1990, Alonso and Whitney 2001, Fitzpatrick 2004). Slow growth has been found in other tropical species that feed fruit to their offspring (Morton 1973). A comparison of the growth rate constant (k) for mass with that published and summarized for other tropical and temperate species (Ricklefs 1976, Willis et al. 1978, Oniki and Ricklefs 1981, Starck and Ricklefs 1998, Remeš and Martin 2002) reveals it is slow even for the slowest growing of tropical tyrannids ($k < 0.3$). Tropical tyrannids from Central America and Brazil had growth rates (k) extending from a low of 0.248 in another species (*Mionectes macconnelli*) that builds enclosed nests (Willis et al. 1978) to rates ≥0.4, similar to those observed for some faster growing tyrannids breeding in North America such as *Tyrannus tyrannus* ($k = 0.438$) and *Sayornis phoebe* ($k = 0.425$) (Murphy 1981), *Tyrannus verticalis* ($k = 0.416$) and *T. forficatus* ($k = 0.394$) (Murphy 1988), *Empidonax minimus* ($k = 0.499$–0.505) (Briskie and Sealy 1989), and *E. oberholseri* ($k = 0.425$) (Pereyra and Morton 2001). Other non-tyrannid passerines investigated in Yacambú National Park also had much higher growth rates (Niklison et al. 2008, Biancucci and Martin 2008, Cox and Martin 2009).

Incubation temperature is a reflection of parental attentiveness with cooler temperatures (low attentiveness) associated with longer incubation period lengths (Lyon and Montgomerie 1985, Martin 2002, Hepp et al. 2006, Martin et al. 2007). The observed 24-hr incubation temperature for *Z. chrysops* is below the optimal temperature range for embryonic growth (White and Kinney 1974, Webb 1987). However, egg temperature was close to the expected value for a tropical species with this length of incubation period and nest attentiveness (Martin et al. 2007: figure 2).

Skutch (1960) considered *Z. vilissimus* in Costa Rica to have high nest attentiveness for a small flycatcher. He observed mean on and off-bouts during incubation of 32.5 and 12.5 min, respectively with overall estimates of attentiveness of 67 and 72%. This indicated higher attentiveness (and shorter off-bouts) for this congener than for *Z. chrysops* in Yacambú National Park. Attentiveness for *Z. chrysops* was in the middle of the range of 39 other species studied in Yacambú (Martin and Schwabl 2008), but was lower than for most temperate passerines (Conway and Martin 2000: appendix 1; Martin 2002; Chalfoun and Martin 2007).

Z. vilissimus had higher provisioning rates than those observed for *Z. chrysops* (Skutch 1960). However, both had mean feeding rates at least two-fold higher than other species studied in Yacambú National Park (Fierro-Calderón and Martin 2007, Biancucci and Martin 2008, Niklison et al. 2008, Cox and Martin 2009). This could reflect compensation for lower protein levels in fruit fed to nestlings (Morton 1973), although flycatchers seem to feed at higher rates than other species (Martin et al. 2000b). Consequently, predation levels could be influenced through greater nest detection due to increased parental visits (Skutch 1949; Martin et al. 2000a, b). However, predation rates were lower during the nestling period than during earlier periods when parents were less active.

Nesting success for *Z. chrysops* was among the lowest observed for a member of the Tyrannidae when compared with other southern hemisphere and neotropical species. Skutch (1985) summarized data from different species in the humid Neotropics showing that 39.7% of nests found were successful with tyrannids exhibiting a range of 12.1 to 50%. *Mionectes oleagineus* in Trinidad had the lowest tyrannid nesting success (12.1%), a trend observed in other small species in Trinidad (Snow and Snow 1979). Low reproductive estimates were observed in *Suiriri islerorum* (≥13.6%, mean = 20.8%) and *S. affinis* (19%) in tropical savannah of Brazil (Lopes and Marini 2005, Franca and Marini 2009). In Costa Rica, 36% of nests of *Zimmerius vilissimus* were successful and fledged chicks (Skutch 1985). Other non-tyrannid neotropical species in Panama were observed to have low nesting success similar to *Z. chrysops* (e.g., some formicariids and a thamnophilid species; Robinson et al. 2000). However, nesting success was generally higher (23–74%) and daily predation rates lower for other tyrannid species in the Neotropics and southern hemisphere; e.g., Argentina (Mezquida and Marone 2001, Auer et al. 2007), Puerto Rico (Torres Báez and Collazo 1992), Brazil (Willis et al. 1978, Aguilar et al. 2000, Medeiros and Marini 2007), and Panama (Robinson et al. 2000, Dyrcz 2002).

The extremely poor nesting success of *Z. chrysops* reflects high predation pressure, and may reflect the tendency for this species to nest

along forest edges where predation levels are high (Söderström 1999). Multiple re-nest attempts would be expected to occur to compensate for high predation (Martin 1995, Fitzpatrick 2004), but the short breeding season (i.e., Fig. 2) and our observations suggest that only 2–3 nesting attempts are made.

The small clutch size of *Z. chrysops* with a relatively long incubation period and slow nestling growth suggest this species is at the 'slow' end of the slow-fast life history gradient (Martin 1996, 2004). The solely neotropical distribution, lack of morphological specialization (Traylor 1977), and indication that only conservative differences in nest architecture occur within the genus, place importance on investigating reproductive parameters of the diversity of *Zimmerius* species. Phenotypic similarity or dissimilarities would be valuable for understanding the finer scale processes influencing reproduction and broader life history variation within tyrannids; e.g., localized predation rates imposed upon otherwise phylogenetically close and similar species (Skutch 1949, 1985; Bosque and Bosque 1995; Martin 1995; Martin et al. 2000a).

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HABITAT TYPE IS RELATED TO NEST MASS AND FLEDGING SUCCESS OF ARCTIC WARBLERS

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ABSTRACT.—Relatively little is known about Arctic Warblers (*Phylloscopus borealis*) that breed in central Alaska. We monitored Arctic Warbler populations in two adjacent but distinct habitat types in central Alaska (high elevation, 'open shrub' and lower elevation, 'dense shrub'). We collected 95 nests over three breeding seasons to learn more about nest-building behavior, nest mass, composition, fledging success, and nest parasites. Females were the sole builders of ground nests, which were primarily comprised of moss, grass, and a lining of moose (*Alces alces*) hair. Dry weight of nests was ~20 g, but differed up to ~3-fold within each habitat type each season. Nests from open shrub habitats were more massive and contained less moose hair lining than nests in dense shrub. Open shrub nests fledged more young during the most productive breeding season. We report the first record of the parasitic blowfly *Protocalliphora tundrae* in Arctic Warbler nests and for Alaska. Blowfly parasitism (55% of nests with hatchlings) was similar in both habitat types and did not correlate with fledging success, or nest mass. Nests with greater amounts of moss tended to have lower levels of blowfly infestation. *Received 26 September 2009. Accepted 10 June 2010.*

The Arctic Warbler (*Phylloscopus borealis*) is an understudied old-world warbler that winters in southeast Asia and has an expansive subarctic breeding range that extends from Norway through Siberia into central Alaska (Tucker 1949, Price and Beck 1989, Lowther and Sharbaugh 2008). Little is known about its cryptic ground-nesting habits throughout its range. Alaska is the only location in North America where Arctic Warblers (Fig. 1A) breed and these populations are considered a separate subspecies (*P. b. kennicotti*) (Lowther and Sharbaugh 2008, Reeves et al. 2008).

Documentation of Arctic Warbler nests in Alaska prior to our observations included a report on 11 nests near Nome (Price and Beck 1989) and two nests in Denali National Park by Murie (1956). Our objectives are to present detailed information about: (1) nest construction, (2) orientation, (3) composition, (4) fledging success, and (5) nest parasites in two adjacent, but distinct habitat types (high elevation, 'open shrub' and low elevation, 'dense shrub') in a central Alaskan population of *P. b. kennicotti*.

METHODS

Study Site.—We studied a breeding population of Arctic Warblers between 2004 and 2006 in the Tangle Lakes region of the Denali Highway in interior Alaska (63° N, 146° W). All data were collected from four 10-ha plots, each 150 m from the Denali Highway at mileposts 23, 26, 30, and 33, respectively. Pairs of plots represented two distinct habitat types of the region. 'Open shrub' plots were at higher elevation (1,121–1,154 m) and included north and east-facing slopes. This habitat type contained meadow-like clearings surrounded by 1–2 m tall willow shrubs (*Salix* spp.) and dominated by gramminoids (*Deschampsia caespitosa* and *Carex* spp.), lupines (*Lupinus arcticus*), and burnet (*Sanguisorba* spp.). Nests were collected from open shrub plots in all 3 years. 'Dense shrub' plots were at lower elevations (910–1,012 m) with flat ground or a gradual, east-facing slope. This habitat type was dominated by dwarf birch (*Betula nana*) and willow. Nests were collected in dense shrub habitats only in 2004 and 2005, as birds typically nested in these locations at much lower densities.

Nest Monitoring, Collection, and Composition.—We located most nests by systematically searching the ground in areas where we observed singing males. Each nest was monitored at least once every 4 days through laying, hatching, and rearing of young. Daily nest checks began 2 days prior to the expected fledging date to ascertain the number of young successfully fledged.

Observations of nest building were made each season and we collected each nest once fledging

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FIG. 1. (A) Color-banded adult Arctic Warbler (*Phylloscopus borealis kennecotti*). Males and females are monomorphic. (Photograph by Ron Teel). (B) Opening of Arctic Warbler nest in the side of a tussock in open shrub habitat. (Photograph by Sue Guers). (C) Nest with fledglings associated with willows in dense shrub habitat. (Photograph courtesy of Alaska Bird Observatory).

was complete (between 20 Jul and 1 Aug). We first recorded nest orientation (in 2005 and 2006 only) by obtaining a compass bearing from a stick inserted straight into the nest opening prior to removing the nest from the ground. Nests are a domed mass of material that can be removed by lifting up the sides and the bottom, once the edge of the nest is located within the surrounding tundra. We carefully removed non-nest material that clung to the outside of the nest during extraction and retrieved any bits of nest material left in the depression. Each nest was placed in a separate plastic collection container for transport to the laboratory, then transferred to a paper sack and dried overnight in an oven at 135° C.

Dry nest mass was measured using an analytical balance. Two key components of nests were measured each year: nest mass and mass of moose (*Alces alces*) hair, which comprised the lining of many nests. Our relatively large sample of nests from open shrub habitat (n = 80) allowed us to examine differences across years. Twenty-six nests from open shrub habitat were dissected further in 2006 to quantify the mass of moss and grass, two key components of nest structure. We calculated the percent composition of hair, moss, or grass as a proportion of nest mass.

A snowstorm on 21 June 2006 caused birds to abandon the eight nests (and clutches) that we had located at that point in the season. However, Arctic Warblers began re-nesting after snow began to melt (on 23 Jun 2006) and we subsequently located 22 new nests. We collected all 30 nests, including the eight that had been abandoned. This sample enabled us to examine any differences between nests built before and after the storm (e.g., With and Webb 1993).

Nest Parasites, Incidental Arthropods, and Fledging Success.—We removed, identified, and counted all puparia of an abundant nest parasite (a blowfly) after nests were dried but before they were weighed. We also identified incidental arthropods. Puparia are the rigid outer shells of developing blowfly larvae. The larval stage obligately feed on the blood of nestlings (Sabrosky et al. 1989). Counting puparia is a conservative measure of parasitism, because it avoids double-counting flies that have successfully pupated into adults. All nests that failed prior to hatching were excluded from analyses (n = 8 that failed during the Jun 2006 storm, n = 3 depredated or abandoned during other years), as puparia only occur after blowfly larvae have fed on nestlings. All arthropod specimens were deposited in the University of Alaska Museum Insect Collection.

Statistical Analyses.—The mass of nest components and parasite counts exhibited strongly non-normal distributions, which made parametric statistics inappropriate. All data are reported as medians and 25–75% interquartile ranges [IQR]. We used Wilcoxon rank sum tests to examine differences in nest construction and fledging success between habitat types. We used Rayleigh tests to ascertain whether orientation of nest openings deviated from a random distribution (Wilkie 1983). We examined differences between years within each habitat type using Kruskal-Wallis ANOVA. We used Spearman's rho (ρ) tests to assess non-parametric correlation(s), including relationship(s) between nest mass, different nest components, fledging success, fledge date, and number of puparia per nest.

RESULTS

Nesting Behavior.—Our observations are based on 95 nests (n = 80 from open shrub habitat, n = 15 from dense shrub habitat) collected over 3 years (n = 24 in 2004, n = 41 in 2005, n = 30 in 2006). All nests were built on the ground with domed roofs and circular side entrances (Fig. 1B), and at times incorporated willow stems (Fig. 1C). Each nest consisted of an outer layer of moss and coarse grass with an inner layer of finer materials including grasses and moose guard hairs, which formed a tightly-compressed, disc-shaped mat upon which eggs were laid.

We witnessed construction of three nests in early June 2005. We observed two color-marked pairs at two nests for ~3 hrs. Males did not carry nesting material or enter the nest during construction. However, males flew to and from nests in close proximity to the female that was gathering nest material. The male perched above the nest while the female entered and built the structure itself. Females typically gathered materials within 100 m of the nest; we did not observe travel between study plots. Chasing and physical interactions between the resident male and other males occurred frequently in the air directly above the nest during construction.

The storm on 21 June 2006 blanketed the study area with 30 cm of snow which persisted for 5 days; eight nests identified at that stage of the season failed. Only one individual at each of six nests was color-marked. Two marked birds

(1 male and 1 unknown, each with an unmarked mate) re-nested in the study area after snowmelt. One nest was depredated, but the other fledged young. We only included the initial nests from the two marked birds in our data set, as re-nests lacked statistical independence.

Nest Construction.—Nests differed noticeably between habitats. Those in open shrub plots were ~30% more massive (n = 68, median [IQR] = 20.7 g [17.3–24.0]) than those in dense shrub (n = 13, median [IQR] = 15.2 g [13.4–20.0]; df = 1, χ^2 = 6.96, P = 0.0083). Nests in dense shrub contained nearly four times the amount of moose hair (n = 13, median [IQR] = 1.1 g [0.4–1.3]) than nests in open shrub (n = 68, median [IQR] = 0.3 g [0.0–0.8]; df = 1, χ^2 = 6.18, P = 0.013).

We measured differences in nest mass up to ~3-fold every season (range: 2.0–3.5 fold) within each habitat. There was no correlation between nest mass and hair mass in either habitat type (open shrub: n = 68, Spearman's $\rho = -0.15$, P = 0.22; dense shrub: n = 13, Spearman's $\rho = -0.02$, P = 0.95). Orientation of nest entrances did not differ from a random distribution (open shrub plots: n = 62, mean vector (μ) = 48°, vector length (r) = 0.13, Rayleigh test Z = 0.82, P = 0.82; dense shrub plots: n = 7, μ = 228°, r = 0.40, Z = 2.02, P = 0.13). Entrances of nests built after the 2006 snowstorm were also randomly oriented (n = 20, μ = 42°, r = 0.26, Z = 1.0, P = 0.37). Mass of nests and moose hair did not differ between pairs of plots within each habitat type (df = 1, $0.055 \leq \chi^2 \leq 1.85$, $0.17 \leq P \leq 0.82$).

Dissection of 26 nests from open shrub habitat in 2006 indicated moss and grass accounted for most of the nest mass (83.4%), and that each was present in similar proportions (median [IQR] = 45.5% [31.0–54.4] and 37.9% [35.9–55.1], respectively). Moose hair, which was primarily incorporated into the nest cup, comprised 2.0% [0.7–4.2] of nest mass. Any remaining mass (~15%, or ~3.0 g) resulted from small pieces of leaves, twigs, and feather dander. Nest mass also correlated positively with moss and grass contained in the nest structure (moss: n = 24, Spearman's ρ = 0.62, P = 0.0013; grass: n = 24, Spearman's ρ = 0.38, P = 0.065).

Nests from open shrub habitat in 2006 were significantly lighter (by 3.2 g or 14.5%) than those from the previous two seasons (median [IQR] 2006: n = 28, 18.9 g [13.9–21.9], 2005: n = 33, 22.1 g [17.4–28.2], 2004: n = 7, 22.1 g [20.8–25.7]; df = 2, χ^2 = 8.13, P = 0.017). The analysis pooled pre-storm (n = 8) and post-storm (n = 20) nests from 2006, as all comparisons (of nest mass, mass of moose hair, moss, grass) failed to reach statistical significance (df = 1, $0.16 \leq \chi^2 \leq 0.44$, $0.51 \leq P \leq 0.68$). Moose hair in nests from open shrub did not differ over 3 years (df = 2, χ^2 = 2.23, P = 0.33). Nest mass and moose hair in dense shrub did not differ over 2 years (2004, 2005; both analyses: df = 1, χ^2 = 0.18, P = 0.67).

Fledging Success, Fledge Date, and Nest Construction.—The median number of young fledged in open shrub habitat differed each year (df = 2, χ^2 = 24.33, $P < 0.0001$). Birds were most successful in 2005 (n = 29, median [IQR] = 6 young [5–6]), followed by 2004 (n = 15, median [IQR] = 4 young [4–5], and the 2006 storm (n = 20, median [IQR] = 4 young [3–5]; pairwise comparisons: df = 1, $4.39 \leq \chi^2 \leq 22.74$, $0.0001 \leq P \leq 0.036$). Open shrub habitat had significantly greater fledging success in 2005 than dense shrub habitat (n = 7, median [IQR] = 3 young [0–6], df = 1, χ^2 = 5.46, P = 0.019). The two habitats did not differ in 2004 (dense shrub: n = 8, median [IQR] = 4 young [3–5], df = 1, χ^2 = 0.018, P = 0.89). We detected no yearly differences in fledging success in dense shrub habitat (df = 1, χ^2 = 0.22, P = 0.64). The two plots within each habitat type also did not differ (df = 1, open shrub: χ^2 = 0.23, P = 0.62; dense shrub: χ^2 = 0.032, P = 0.86).

Median fledge date in open habitat differed significantly between years (n = 14, 2004: 20 July; n = 32, 2005: 22 July; n = 20, 2006: 27 July; df = 2, χ^2 = 34.49, $P < 0.001$). The storm disrupted breeding in 2006 and resulted in a median fledge date that was 5–7 days later than in previous years (df = 1, χ^2 = 13.48, $P < 0.001$). Median fledge dates in dense shrub habitat were identical to those reported for 2004 and 2005.

Nest mass in open shrub habitat correlated positively with three measures of reproductive success when all years were combined (n = 60, young fledged per nest: Spearman's ρ = 0.28, P = 0.039; young hatched: Spearman's ρ = 0.33, P = 0.012; clutch size: Spearman's ρ = 0.30, P = 0.024). Nest mass also correlated negatively with fledge date (n = 60, Spearman's $\rho = -0.26$, P = 0.05). The relationships were not detectable, however, when the disrupted 2006 season was excluded (n = 44, $0.03 \leq$ Spearman's $\rho \leq 0.09$, $0.60 \leq P \leq 0.86$), or when each year was analyzed separately ($7 \leq n \leq 33$, $-0.48 \leq$

Spearman's $\rho \leq 0.15$, $0.27 \leq P \leq 0.74$). Hair mass in open shrub nests did not correlate with any measure of reproductive success ($n = 60$, $-0.11 \leq$ Spearman's $\rho \leq 0.12$, $0.35 \leq P \leq 0.49$). Nest mass, hair mass, reproductive success or fledge date of nests from dense shrub had no detectable relationships ($7 \leq n \leq 14$, $0.078 \leq$ Spearman's $\rho \leq 0.20$, $0.52 \leq P \leq 0.80$).

Nest Parasites, Incidental Arthropods, and Fledging Success.—We extracted 1,241 parasitic blowfly puparia and 187 adults from Arctic Warbler nests. The blowfly was identified as *Protocalliphora tundrae*. Incidental arthropods included three families of beetles (Order: Coleoptera) (Leiodidae: *Catops alpinus*, Carabidae: *Patrobus foveocollis*, Staphylinidae: *Quedius brunnipennis*).

Forty-six of 84 nests that successfully hatched young (55%) contained blowfly puparia, and the proportion of parasitized nests was similar in both habitats (open shrub habitat: 39 of 70 [56%], dense shrub: 7 of 14 [50%]). Most nests contained few puparia (median [IQR] = 1 [0–22]). The greatest number of puparia recorded in one nest was 157 (from open shrub habitat in 2006). Blowfly parasitism did not differ by habitat type (open shrub plots: $n = 69$, median [IQR] = 1 [0–23]; dense shrub plots: $n = 14$, median [IQR] = 1 [0–13]; df = 1, $\chi^2 = 0.29$, $P = 0.59$) or by study plot (df = 3, $\chi^2 = 3.76$, $P = 0.29$). There was no correlation between puparia count per nest and fledging success ($n = 81$, Spearman's $\rho = -0.056$, $P = 0.62$) or nest mass ($n = 73$, Spearman's $\rho = 0.12$, $P = 0.29$).

Parasite incidence per nest in open shrub habitat differed significantly between years with nests in 2004 containing few puparia ($n = 15$, median [IQR] = 0.0 [0.0–0.0]) compared to those in 2005 ($n = 33$, median [IQR] = 4 [0–28] and 2006 ($n = 21$, median [IQR] = 12 [0–28]; df = 2, $\chi^2 = 15.74$, $P = 0.0004$). The mass of moss contained in open shrub nests tended to be negatively associated with puparia count ($n = 17$, Spearman's $\rho = -0.45$, $P = 0.07$). Nests from dense shrub plots had no correlations between nest characteristics (mass, hair), puparia count, or young fledged ($12 \leq n \leq 13$, $-0.07 \leq$ Spearman's $\rho \leq 0.26$, $0.40 \leq P \leq 0.83$).

DISCUSSION

Nesting Behavior and Nest Composition.—The 95 nests we examined add new details to our understanding of Arctic Warblers that breed in central Alaska. First, consistent with other studies of *Phylloscopus* warblers, including other populations of *P. borealis* (Barlein 2006, Clement 2006), females are the primary, if not sole, nest builder while males sing nearby and defend the site. Second, nests weigh ~20 g, and over 83% of nest mass is attributable to moss and grass. Our observations of nest location, shape, and lining of animal hair are consistent with other reports from Alaska (Murie 1956, Price and Beck 1989), and other *Phylloscopus* species (Bi 2004). Third, our data indicate nest openings were randomly oriented. Exposure can influence a nest's microclimate (With and Webb 1993), and several ground-nesting species exhibit clear patterns with regard to orientation, including birds that build domed nests or breed at high latitudes (e.g., Burton 2007, Long et al. 2009). The position of openings of Arctic Warbler nests may be based on other parameters that we did not measure, including shelter near the nest site. It is also possible orientation is opportunistic given the uneven topography of tundra hummocks.

Nest Construction.—Nests in open shrub habitat were more massive and contained less moose hair lining than those in dense shrub. Two non-exclusive explanations may account for this result. We hypothesize that local availability of nest materials differs between habitat types. For example, we often saw moose hair snagged on branches in dense shrub habitat, but moose were less common and had less opportunity (fewer shrubs of adequate height) to snag hair in open shrub habitat. The extensive breeding range and variety of nesting habitats of *Phylloscopus borealis* (Lowther and Sharbaugh 2008) are also consistent with an opportunistic focus upon local resources during nest building (Barlein 2006).

An inverse relationship between nest mass and moose hair is suggestive of a thermal trade-off between the two habitat types. Pilot studies conducted on nests *in situ*, but after fledging, failed to detect any positive correlation between nest mass or the mass of moose hair lining and the insulation quality of nests ($n = 41$ nests, unpubl. data). We believe this warrants additional research, preferrably during incubation or brooding, as thermal properties likely result from a combination of factors, including amount and kind(s) of nest material, local topography of the breeding site, and parental behavior (Skowron and Kern 1980).

Fledging Success, Fledge Date, and Nest Construction.—Habitat type was associated with

a measurable difference in fledging success. Birds in open shrub plots during 2005 fledged twice the number of young as those in dense shrub. Open shrub plots at our study site also had a greater nest density (Sharbaugh et al. 2007), which supports the conclusion that open shrub habitat is generally more favorable to Arctic Warblers.

The snow storm on 21 June 2006 interrupted breeding, as the median fledge date in 2006 occurred 5–7 days later than previous years. Nests were significantly lighter only in 2006, suggesting birds built somewhat smaller nests due to the shortened season caused by the storm. We detected no difference, however, between nests built before and after the 2006 storm, possibly due to our small sample of pre-storm nests ($n = 8$).

It is unclear why Arctic Warblers exhibit such striking (~3-fold) differences in nest mass within each habitat type. Nest mass correlated positively with fledging success and negatively with fledge date in open shrub habitat when all years were combined. These patterns were no longer evident, however, when the disrupted 2006 season was removed, or in smaller (yearly) samples. Nest mass in other avian species can indicate quality of the female nest builder (e.g., Soler et al. 1998, Mainwaring et al. 2008), or enhanced parenting effort (e.g., Szentirmai et al. 2005, Broggi and Senar 2009).

Nest Parasites, Incidental Arthropods, and Fledging Success.—The puparia collected represent the first Alaska record of the avian blowfly *Protocalliphora tundrae*. Our observations increase the number of known avian hosts of *P. tundrae* from two (Snow Bunting [*Plectrophenax nivalis*] and Savannah Sparrow [*Passerculus sandwichensis*]) to three, all of which are ground-nesting birds (Sabrosky et al. 1989). *P. tundrae* is considered a rare tundra inhabitant of northern Canada and the Yukon (Sabrosky et al. 1989). Incidental arthropods included *Catops alpinus*, a dung and carrion scavenging beetle known to occur in alcid nests (Perreau 1998, Peck and Cook 2002), and two other beetles that are generalist predators (*Patrobus foveocollis* and *Quedius brunnipennis*). *Q. brunnipennis* in Alaskan tundra is unusual, as it has been reported to be a mature forest specialist from Alberta (Pohl et al. 2007).

Blowfly parasitism of young varied annually but did not correlate with fledging success. This result is consistent with both observational and experimental investigations of other *Protocalliphora* species and passerine hosts (Roby et al. 1992, Wittmann and Beason 1992). One recent investigation, however, suggests blowflies contribute to mortality and reduced movement soon after fledging (Strebyl et al. 2009).

There are at least two different, non-exclusive explanations for the negative relationship between blowfly puparia and moss mass that warrant future study. First, moss may create a cool microhabitat. Cool environments can cause *Protocalliphora* to delay or fail during larval development (Bennett and Whitworth 1991). Second, moss may cause nests to retain moisture, and *Protocalliphora* larvae, unlike other blowflies, survive poorly when humidity is high (Bennett and Whitworth 1991).

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HOME RANGE, HABITAT USE, AND NEST SITE CHARACTERISTICS OF MISSISSIPPI KITES IN THE WHITE RIVER NATIONAL WILDLIFE REFUGE, ARKANSAS

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ABSTRACT.—We located 39 Mississippi Kite (*Ictinia mississippiensis*) nests during the 2004 and 2005 breeding seasons in the White River National Wildlife Refuge in the Mississippi Alluvial Valley of Arkansas, USA. Radio transmitters were placed on seven adult and eight juvenile kites; 649 locations based on ground telemetry and 393 locations from aircraft were recorded for six adults (n = 5 males, 1 female) and five juveniles (n = 2 males, 3 females). The mean 90% kernel home range was 3,098 ha for adult kites (n = 6) and 439 ha (n = 5) for juveniles. Radio-marked Mississippi Kites significantly used mature forest (65.6%), second growth (15.5%), and water (10.0%) relative to availability (59.6, 11.5, and 7.1%, respectively). Agriculture fields (6.5%) and wetlands (1.5%) were used significantly less within the home ranges of kites relative to availability (17.6 and 3.9%, respectively). Tree height, diameter at breast height (dbh), and height of nest tree emergence above the surrounding trees were significantly greater for nest sites than randomly-selected overstory trees. Nest trees were significantly closer to the edge than randomly-selected trees. Most (57%) Mississippi Kite nests were in crotches of secondary branches in the nest tree. Conservation of super-emergent trees and mature forests is needed for nesting and foraging areas. Second-growth forest should be allowed to mature (>75 years) and uniform canopies should be avoided. *Received 7 August 2009. Accepted 28 April 2010.*

The Mississippi Kite (*Ictinia mississippiensis*) breeds in bottomland and riparian areas throughout the Mississippi River Valley and southeastern North America (e.g., Kalla 1979, Evans 1981, Whitmar 1987, Barber 1995, St. Pierre 2006). This raptor also inhabits riparian areas, shelterbelts, oak (*Quercus* spp.)-shrub prairies, and savannas in the western United States (Parker 1988). This kite has adapted to nesting in urban golf courses, parks, and neighborhoods primarily in the western portion of its range (Parker 1988). The ability of the western population to adapt to encroachment of humans has allowed it to increase in number and expand into new areas (Parker and Ogden 1979).

Kite populations in the eastern United States were affected by severe habitat alteration in the late 1800s and early 1900s. Gosselink and Lee (1989) estimated that, at time of European settlement, there were ~80 million ha of forested freshwater wetlands in the United States with the majority in the Mississippi Alluvial Valley. The area of bottomland hardwood forests in the Mississippi Alluvial Valley decreased to 4.8 million ha by 1937, and to only 2.1 million ha by 1970 (Gosselink et al. 1990).

Several researchers have described habitat use and nest site characteristics of Mississippi Kites, often based on small sample sizes, in Tennessee (Kalla 1979), Illinois (Evans 1981), Missouri (Whitmar 1987, Barber 1995), and Arkansas (St. Pierre 2006) within the Mississippi Alluvial Valley; almost all of this work remains unpublished. Allan and Sime (1943) observed daily activities of 169 Mississippi Kites in the panhandle of Texas and subjectively estimated home-range size to be ~250 ha. Barber (1995) using telemetry estimated mean home-range size of kites along the Mississippi River in Missouri as 1,160 ha (n = 10), much larger than estimates from the Texas panhandle. Barber (1995) compared the number of telemetry locations within specific vegetation types to estimates of the proportions of these types available in the surrounding landscape.

Forested habitats fragmented with agricultural fields and developments are not ecologically equivalent to the relatively contiguous-forested habitats once used by kites in the 1800s and early 1900s. The vast changes in the landscape probably affected home-range size and habitat use, and may have influenced reproductive success of this species (Bader and Bednarz 2009). A better understanding of how Mississippi Kites use landscapes that are present today will be useful to conserve and enhance habitats for this species. Our objectives were to examine: (1) use of habitats and landscapes, and (2) selection of nest sites by Mississippi Kites in the Mississippi Alluvial Valley.

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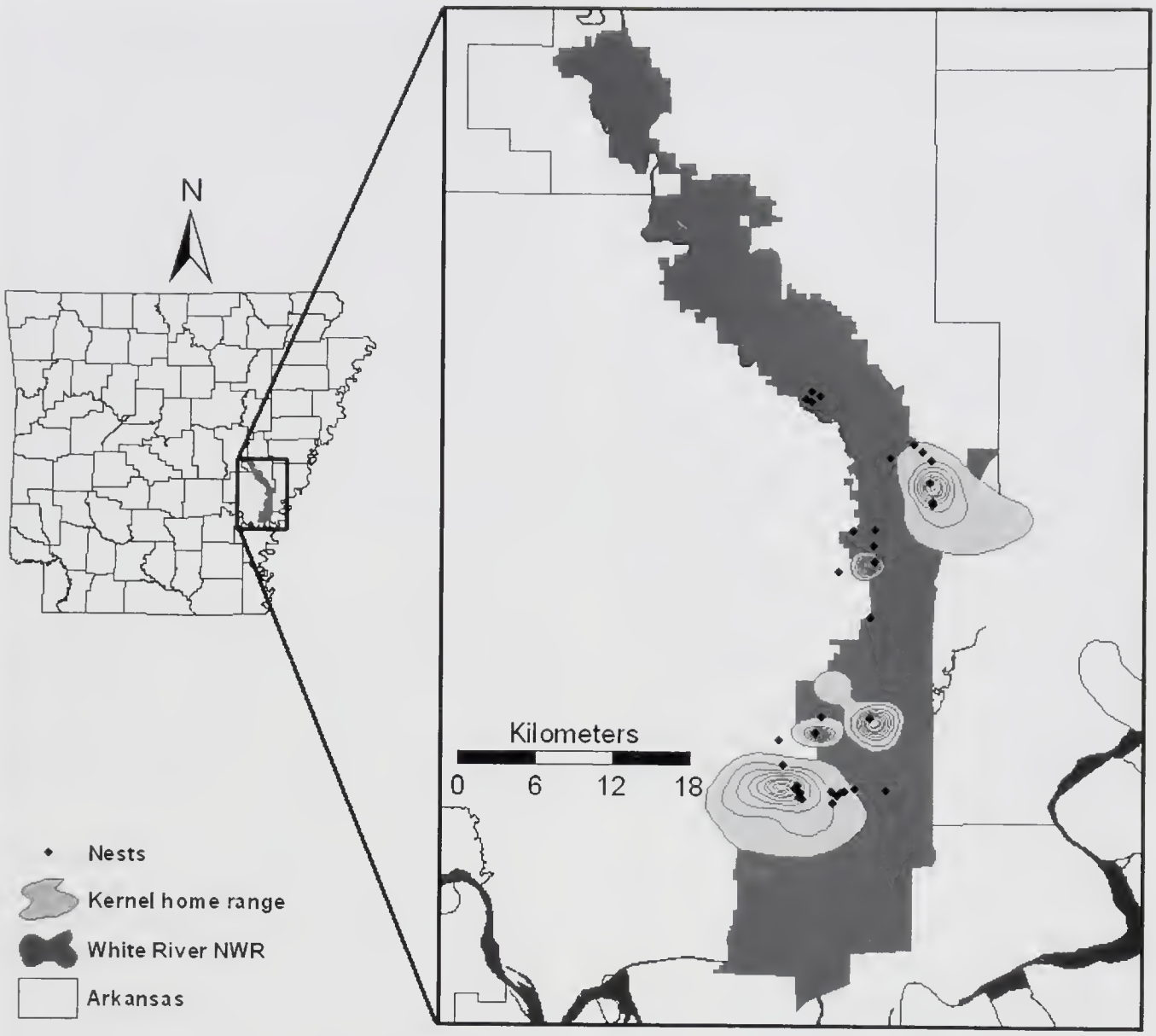

FIG. 1. Nest locations (n = 39) and kernel home ranges (n = 5) of adult Mississippi Kites in the White River National Wildlife Refuge and vicinity in Arkansas, 2004–2005.

METHODS

Study Area.—White River National Wildlife Refuge (WRNWR; Fig. 1) is in Arkansas, Desha, Monroe, and Phillips counties in southeastern Arkansas. It is ~64,750 ha in size and is divided into two units by Arkansas Highway 1. The South Unit, where the majority of our work was conducted, is the larger of the units (41,440 ha). This unit extends from St. Charles, Arkansas south to the confluence of the White River and the Arkansas River Canal (Fig. 1). The WRNWR consists mostly of bottomland hardwoods open to the public for recreational use, hunting, and fishing and is managed for both game and non-game wildlife species (Bader 2007).

Nest Searching.—We began searching for Mississippi Kite nests on 9 and 23 April 2004 and 2005, respectively. Once a Mississippi Kite was located, we watched it for possible breeding activities such as carrying sticks or copulation, which indicated kites were nesting nearby. We recorded the location of each nest with a Global Positioning System (GPS) receiver and left the site immediately to minimize disturbance. We periodically returned to areas where Mississippi Kites were seen and continued searching until a nest was found or kites abandoned the area, indicating they were no longer attempting to breed.

Capturing and Radio-marking Kites.—We used a mist-net system with a live Great Horned Owl (*Bubo virginianus*) or Red-shouldered Hawk (*Buteo lineatus*) near nests with nestlings (7–30 days of age) to capture adult Mississippi Kites

(Hamerstrom 1963, Barber et al. 1998). The mist-net system consisted of two 2.6 × 6 m mist nets (72 mm mesh) connected to a pulley system on telescoping metal poles. This allowed the top of the net to be elevated ~7 m above ground with the bottom of the lower net ~1.5 m off the ground. The total dimensions of the system using two mist nets were 5.2 m in height × 6 m wide (Bader 2007).

We placed a U.S. Geological Survey (USGS) aluminum band and two or three plastic color bands on legs of each kite for unique identification. Selected kites were also fitted with a radio transmitter using a modified figure-eight leg harness (Radley 2002). Mississippi Kites were fitted with a 6.0-g transmitter (Holohil Systems Ltd., Carp, ON, Canada). We recorded several linear measurements, mass, and obtained a blood sample from each kite, before it was released. Gender of each kite was assigned based on plumage characteristics (Parker 1999), and verified by DNA analysis in the laboratory (Bader 2007). We left the nest site immediately once a kite was released to minimize any potential stress on adult and nestling kites.

We climbed to each nest and banded the nestling(s) when they were 3–4 weeks of age. The mass of each nestling was measured, and a USGS aluminum band and two or three plastic color bands were placed on their legs for identification of individuals. Each nestling was also fitted with a radio transmitter using the procedure described for adults and returned to the nest.

Gender Identification.—A 0.05-cc sample of blood was drawn from the brachial vein of each kite using a hypodermic needle and a small capillary tube (Faaborg et al. 1995) and placed in Longmire Solution (Longmire et al. 1988). The protocol outlined by Donohue and Dufty (2006) was followed to extract DNA from the blood and isolate the CHD-Z and CHD-W bands (Griffiths et al. 1998) to identify the gender of captured kites.

Radiotelemetry of Adult and Juvenile Kites.—Triangulation was used to obtain locations from the ground and a fixed-wing aircraft was used to identify point locations from the air. Receiver sites for triangulations were established ~500 m apart along roads or all-terrain vehicle trails near nest sites and compass azimuths were recorded in the direction of the strongest signal from the radio-marked kite. Compass azimuths from at least three receiver sites were taken within a 5-min period to estimate the error ellipse around each location. Eight triangulations with a ≥10-min interval between each triangulation were completed 2–3 days each week. The 10-min period allowed time for the kite to move between triangulation attempts, minimizing autocorrelation between locations (Swihart and Slade 1985). The triangulation azimuth was entered into the OTA Triangulation Program (Ripper et al. 2007), which provided coordinates for the estimated location. We could calculate an error ellipse using this program that theoretically has a 95% probability of including the true location of the kite. We eliminated all estimated locations that had an error ellipse greater than 10 ha to improve accuracy. This relatively large error ellipse criteria was chosen to accommodate the high mobility of kites (typical home range size >3,000 ha).

We obtained locations from the air (DeVault et al. 2003) for each radio-marked kite 2–3 times per flight depending on the amount of flight time available. Locations of individual kites were recorded >20 min apart. Flights were conducted 2–3 days each week using a Cessna 172 or 182 equipped with a pair of "side-looking" 4-element yagi antennae (Bader 2007).

Habitat Use.—Point locations were entered into Geographic Information System (GIS) ArcView software and home-range polygons were developed for each kite. Two types of home-range polygons were generated using point locations: minimum convex polygon (MCP) and 90% kernel (White and Garrott 1990). We used the 90% probability of use contours as estimates of home-range size. The home-range polygon of each kite was overlaid onto USGS Digital Orthophotograph Quarter Quadrangles (DOQQs) taken in fall 2004.

ArcMap 8.3 at a scale of 1:3,000 was used to classify habitats into seven cover types within each home range. The mature forest cover type consisted of tracts of large trees that had relatively even canopy with few openings and had not been recently logged (>30 year). Second-growth cover type consisted of young forest with large openings in the canopy, abandoned fields, and recently-logged forest. The water cover type included all open waterways (e.g., lakes, bayous, and rivers). The wetland cover type included all forested and non-forested swamps and low-lying vernal areas. The agriculture cover type included all types of agriculture fields (e.g., crop and hay fields). The urban cover type consisted of noticeably developed areas (e.g., rural towns). The road cover type

included highways, county roads, and obvious private roads. Polygons were drawn around each cover type and the sum of all polygons within a cover type was used to calculate the number of hectares available of that cover type within a given home range.

Bailey's confidence intervals (Bailey 1980, Cherry 1996) were used to examine whether kites used cover types within their home range in proportion with that available. We used the Chi-square distribution and a Bonferroni correction based on the number of available cover types to construct a 95% confidence interval (CI) around the proportion of telemetry locations within each cover type. The confidence interval was compared to the proportion of habitat that was available within the kite's home range to delineate the level of kite use.

Nest-site Characteristics.—Vegetation data were collected at every nest site after young fledged or the nest failed and at an equal number of sites selected using a random-number table. The distance (0–250 m) was paced while using a compass to follow the random azimuth to locate the reference sample site and the closest overstory tree was chosen as the plot center. The same vegetation data were collected within a 0.04-ha circular plot around nest and random trees. We followed the BBIRD Protocol (Martin et al. 1997) and included species of the tree, tree height, tree diameter at breast height (dbh), distance to forest edge, dominant and co-dominant trees within the surrounding area, and species and height of each tree in the overstory and within the circular plot. Data collected on nest-site characteristics included nest height, orientation of nest in tree, and position of nest in tree (primary or secondary fork).

We collected data on perch trees, defined as the tree(s) in which kites perched in the morning and frequently during the day in the immediate vicinity (<200 m) of their nests. Measurements collected at perch trees were the same as those taken for nest trees, but also included distance from nest and azimuth to nest. We recorded whether the tree was dead or alive and classified it as a primary or secondary perch tree. The primary perch tree was the tree that one or both kites used the majority (>50%) of the time. The secondary perch tree, if present, was the tree used by one or both kites less frequently (<50%).

Statistical Analysis.—We used a paired *t*-test (SAS Institute 1999) to compare Mississippi Kite nest sites with sites selected at random (Sokal and Rohlf 1995), and a *t*-test to compare characteristics of primary and secondary perch trees.

RESULTS

We located 21 Mississippi Kite nests in 2004 and 18 in 2005. We captured seven adult kites, each from separate nests (4 in 2004, 3 in 2005), in 22 trapping attempts. We made 11 attempts to capture chicks in 2004 and 2005 and captured nine (at ages of ~3.5–4 weeks) from nine nests.

Analysis of DNA to identify gender of captured adult and nestling kites was conducted on 14 blood samples (6 adults and 8 nestlings). Five male and one female adult kites, and four male and four female nestling kites were identified. Five of six adults (83%) were identified correctly to gender based on plumage coloration.

Radio-marked Mississippi Kites were located using ground receiver sites from 9 July to 28 August 2004 and from 14 July to 20 August 2005. Locations of each radio-marked kite were recorded from a fixed-wing aircraft from 28 July to 19 August 2004 and from 20 July to 26 August 2005. We recorded 649 locations from the ground (2004 = 449 locations, 2005 = 200 locations) and 393 locations from the air (2004 = 134 locations, 2005 = 259 locations).

MCP and 90% kernel home ranges were generated for each radio-marked kite (Table 1, Fig. 2). The mean (± SE) MCP home range size for adult male radio-marked kites was 3,289.1 ± 1,419.3 ha; n = 5). Home-range data were collected for only one female and the MCP home range was 1,899.8 ha. The mean (± SE) MCP home range for male juvenile kites was 536.2 ± 10.8 ha; n = 2) and 508.4 ± 316.4 ha; n = 3) for female juvenile kites. The mean (± SE) home range using the 90% kernel method for adult male radio-marked kites was 3,567.3 ± 1,393.5 ha; n = 5). The home range size for the one radio-marked adult female kite using the 90% kernel method was 752.2 ha. The mean 90% kernel home range for male juvenile kites was 299.0 ± 23.0 ha (n = 2) and 533.0 ± 266.7 ha (n = 3) for female juvenile kites.

We estimated habitat use within home ranges of 12 Mississippi Kites (6 adults, 6 juveniles). Mississippi Kites significantly used mature forest (95% CI = 0.611–0.698; Table 2) more than its availability (0.596). Water was also significantly used (95% CI = 0.074–0.130; Table 2) more relative to its availability (0.071). Mississippi

TABLE 1. Minimum convex polygon (MCP) and 90% kernel home range data for Mississippi Kites radiotracked in the White River National Wildlife Refuge, Arkansas, 2004–2005.

Band #	Gender	Age[a]	# of triangulations	# of aerial locations	Total locations	MCP (ha)	90% Kernel (ha)	Year
745-57320	M	AHY	32	20	52	1,398.64	1,594.23	2004
745-57323	F	HY	53	17	70	78.37	55.75	2004
745-57318	F	AHY	103	21	124	1,899.81	752.19	2004
745-57322	M	HY	47	19	66	547.00	321.96	2004
745-57319	M	AHY	112	18	130	626.10	431.14	2004
745-57321	F	HY	48	19	67	1,125.44	975.75	2004
745-57324	M	AHY	54	20	74	6,225.47	7,770.00	2004
745-57326	M	AHY	95	60	155	7,235.58	5,896.23	2005
745-57327	M	AHY	22	13	35	959.68	2,145.07	2005
745-57329	F	AHY	5	18	23[c]	497.44	1,192.65	2005
745-57328	M	HY	0	11	11[d]	0	0	2005
745-57331	M	HY	35	72	107	525.42	275.94	2005
745-57332	–[b]	HY	10	26	36[c]	548.27	545.45	2005
745-57330	F	HY	33	61	94	321.37	567.61	2005
745-57333	F	HY	0	0	0[e]	0	0	2005

[a] AHY = after hatch year or breeding adult; HY = Hatch year or nestling.
[b] No blood was collected.
[c] Few locations because kite was depredated (not included in calculation of MCP or kernel means).
[d] Locations while chick was still in the nest (not included in calculation of MCP or kernel means).
[e] No data collected before nestling was depredated (not included in calculation of MCP or kernel means).

Kites also significantly used second growth (95% CI = 0.123–0.190; Table 2) more relative to its availability (0.115). Agriculture fields and wetlands were significantly used less relative to availability (Table 2). Mississippi Kites used both roads and urban areas in proportion to their availability (Table 2).

The mean nest tree height (33.26 m) was significantly taller (t = 5.37, df = 33, P < 0.0001; Table 3) than paired randomly-selected trees (26.77 m). Mean dbh of nest trees (75.58 cm) was significantly greater (t = 8.44, df = 33, P < 0.0001; Table 3) than paired randomly-selected trees (48.34 cm). Mean height of nest-tree emergence (5.29 m) above the surrounding canopy was significantly greater (t = 3.44, df = 33, P = 0.0016; Table 3) than the mean height of randomly-selected tree emergence (0.70 m). The mean (± SE) height of Mississippi Kite nests was 26.89 ± 0.82 m, while the mean surrounding canopy height was 27.68 ± 0.74 m, indicating kites tended to build nests almost level with the height of the surrounding canopy.

The mean (± SE) distance (61.06 ± 15.65 m) to the forest edge from Mississippi Kite nests was significantly less (t = 4.16, df = 33, P = 0.0002; Table 3) than the distance (126.19 ± 16.18 m) to the forest edge from randomly-selected sites. Other measured variables did not differ between nest and random sites (Table 3).

Twenty of 35 nest sites (57%) were in crotches of secondary branches. The remaining 15 nests were on primary branches of nest trees. Nests were randomly placed in any direction throughout the nest trees. Mississippi Kite nests were found in six species of trees with Overcup oak (*Quercus lyrata*; n = 11) used most commonly. Sweetgum (*Liquidamber styraciflua*; n = 7), willow oak (*Q. phellos*) (n = 7), Nuttall oak (*Q. nuttallii*; n = 3), American sycamore (*Platanus occidentais*; n = 2), and white oak (*Q. alba*; n = 1) were used less frequently as nesting sites.

Mississippi Kites used numerous species of trees for perching. Black willow (*Salix nigra*; n = 9) and water hickory (*Carya aquatica*; n = 8) were the two most common species used for primary perches. Overcup oak (n = 5) and Nuttall oak (n = 4) were also commonly used for primary perches. Sweetgum (n = 3), slippery elm (*Ulmus rubra*; n = 3), willow oak (n = 2), and water oak (*Q. nigra*; n = 2) were also used as primary perch trees. Nineteen (52.8%) of 36 primary perch trees (Table 4) were live with a dead limb used as the perch, six were live trees with sparsely-leaved limbs, six were live trees with live limbs used as perches, and five were dead trees.

Secondary perch trees included water hickory (n = 3), overcup oak (n = 2), water oak (n = 1), and sugarberry (*Celtis laevigata*; n = 1). One dead tree, three live trees with sparsely-leaved

FIG. 2. Minimum Convex Polygon (MCP) and 90% kernel home range of a radio-tracked Mississippi Kite (Band # 745-57331) in the White River National Wildlife Refuge, Arkansas, 2005.

TABLE 2. The proportion of cover types within home ranges available and used by radio-tracked adult (n = 6) and juvenile (n = 6) Mississippi Kites in the White River National Wildlife Refuge, Arkansas, 2004–2005.

Cover type	ha	Locations in cover type	Proportion of cover type available	Proportion of observed use	95% Confidence Interval of use
Agriculture	3,683.83	57	0.176	0.065*	0.044–0.090
Mature forest	12,497.36	577	0.596	0.656*	0.611–0.698
Second growth	2,417.41	136	0.115	0.155*	0.123–0.190
Road	64.83	2	0.003	0.002	0.000–0.011
Wetland	821.65	13	0.039	0.015*	0.006–0.029
Urban	38.59	6	0.002	0.007	0.001–0.018
Water	1,488.13	88	0.071	0.100*	0.074–0.130

* Significantly different from amount available.

limbs, two live trees with a dead limb, and one live tree with live limbs were all used as secondary perch trees.

There were no significant differences in dbh, tree height, distance to edge, or distance to nest between primary and secondary perch trees (Table 4). Primary and secondary perch trees were significantly closer (t = 5.6, df = 37, P = <0.001) to an edge and had a significantly larger (t = 7.5, df = 34, P < 0.0001) dbh than trees selected at random (Tables 3, 4). There was no significant difference in height of primary and secondary trees and trees selected at random.

DISCUSSION

The mean 90% kernel home range size of male Mississippi Kites (3,567 ha, n = 5) was larger than the one female monitored (752 ha). We suggest this difference may be real because males are more likely to venture long distances from the nest during their daily foraging activities (Dunstan et al. 1978, Barber 1995). Males range widely, probably to gain access to habitat types or food resources that are not available near the nest site. Access to a larger foraging area and possibly to areas with more abundant prey makes the male's role as a food provider to the nestlings vital to success of the nest. Female kites may have smaller home ranges because of their role in the primary defense of the nest; they also tend to the nestlings more than males, similar to other female raptors (Newton 1978, Collopy 1984, Bader 2007).

Barber (1995) estimated the mean male MCP Mississippi Kite home range size in Missouri as 1,357 ha (n = 6), notably smaller than the mean male MCP home ranges that we estimated (3,289 ha). The mean female kite home range in Missouri was 865 ha (n = 4; Barber 1995), also considerably smaller than the MCP home range of the one female that we radiotracked (1,900 ha). We suggest these difference may be due to either differences in landscapes of the respective study areas (the Missouri study was conducted in a more fragmented, forest-agriculture landscape) and the techniques used (no aerial telemetry was used in the Missouri study), or both factors.

TABLE 3. Habitat characteristics at Mississippi Kite nest sites (n = 39) and sites selected at random (n = 39) in the White River National Wildlife Refuge, Arkansas, 2004–2005.

Variable	Nest site		Random site		
	Mean ± SE	Range	Mean ± SE	Range	P[a]
Tree height (m)	33.26 ± 0.97	24.09–43.07	26.77 ± 0.92	14.30–41.42	<0.0001*
DBH (cm)	75.58 ± 3.32	52.70–113.80	48.34 ± 2.25	20.30–79.00	<0.0001*
No. of trees in 0.04-ha plot	3.56 ± 0.30	1.00–7.00	3.53 ± 0.31	1.00–8.00	0.9378
Mean tree height[b] (m)	27.68 ± 0.74	20.77–37.57	26.85 ± 0.72	20.25–37.32	0.3535
Tree emergence[c] (m)	5.29 ± 0.93	−8.53–17.85	0.70 ± 0.76	−11.20–9.39	0.0016*
Distance to forest edge (m)	61.06 ± 6.13	0–142.50	126.19 ± 16.18	0–311.00	0.0002*

* Significantly different from sites selected at random, $P \leq 0.05$.

[a] P = probability that means are different based on a paired t-test.

[b] Mean tree height = mean height of trees in a 0.04-ha plot surrounding the nest or random tree.

[c] Tree emergence = the difference between mean height of nest trees above surrounding trees in 0.04 ha plot or mean height of random trees above surrounding trees in 0.04-ha plot.

TABLE 4. Characteristics of primary (n = 36) and secondary (n = 7) perch trees of Mississippi Kites in the White River National Wildlife Refuge, Arkansas, 2004–2005.

Variable	Primary		Secondary	
	Mean ± SE	Range	Mean ± SE	Range
Tree height (m)	30.41 ± 1.68	14.3–66.5	27.23 ± 3.31	18.6–41.46
DBH (cm)	74.45 ± 2.77	36.1–111.8	84.14 ± 7.43	55.5–103.8
Distance to nest (m)	82.68 ± 8.66	11.3–231.0	78.53 ± 10.02	45.0–120.0
Distance to edge (m)	18.74 ± 3.17	0–77.3	29.89 ± 16.49	0–124.5

Our data documented that Mississippi Kites significantly used open waterways more than available to kites within their home ranges (Table 2). Open water likely provided habitat for prey items such as dragonflies (Odonata) and frogs (Anura). Barber (1995) did not report this cover type to be more abundant within kite home ranges compared to reference areas, but it was a large part of most home ranges that he sampled.

Agricultural fields were used less within the kite home ranges in Arkansas than available (Table 2), but were significantly more abundant in kite home ranges in Missouri (Barber 1995). Soybeans, milo, corn, cotton, and fallow fields were included in the agriculture cover type in the Missouri study. Rice, soybeans, and cotton were the primary crops farmed in the areas surrounding the WRNWR.

Wetland areas were significantly underused (Table 2), but we suggest wetlands indirectly may be an important area for foraging kites. Wetlands likely produce prey, but this prey is not restricted to these areas and probably moves into other cover types where kites may forage on them. Wet areas are used as foraging habitats by other raptors such as the Red-shouldered Hawk (Bednarz and Dinsmore 1981, Bloom et al. 1993, Howell and Chapman 1997).

Mature forests were significantly used more within the home ranges of Mississippi Kites in Missouri (Barber 1995) and in Arkansas (Table 2). In Tennessee, Kalla (1979) reported wooded areas in the floodplain provided preferred nesting sites for kites and key habitat for prey species. Mature forests provide habitat for dragonflies and cicadas (Homoptera), the two most common prey items delivered to nests in the WRNWR (Bader 2007). Red-shouldered Hawks were demonstrated to use forested habitats in California (Bloom et al. 1993) and bottomland hardwood forests in Georgia (Howell and Chapman 1997) more than available. Large contiguous tracts of mature forests seem to be an important cover type for kites providing both nest sites and prey.

Second growth was used significantly more within home ranges of kites in Arkansas (Table 2), but not in Missouri (Barber 1995). This cover type is common in numerous landscapes, and can provide foraging habitat and marginal nesting habitat for kites. Timber stands classified as second growth can provide nest sites if super-emergent trees are not removed during timber harvest operations or are created during timber harvest. Fallow fields, which consist of early successional growth, can provide habitat for aerial insects and other prey items. The second growth cover type was not common in kite home range in Missouri and only accounted for 3.8% of home ranges and 1.2% of the sampled surrounding areas.

Kites used urban areas and roads in proportion to availability within their home range. Both urban areas and roads were near other cover types used by kites. Kites may have used thermals produced in these areas and probably did not actively select these sites for foraging.

Mississippi Kites selected trees taller than the mean overstory canopy height for their nest tree (Table 3). Use of super-emergent trees for nesting allows this long-winged raptor efficient access to the nest (Barber et al. 1998). Kites in WRNWR tended to build nests almost level with the top of the surrounding canopy. Barber (1995) and Whitmar (1987) reported nests were higher than the tops of the surrounding trees. Placing nests at or slightly above the tops of the surrounding trees may provide a view of the surrounding area and potential predators (Whitmar 1987, Barber 1995). Placing nests slightly below the surrounding canopy height would give the nest more protection from the wind and make the nest less conspicuous to predators. Mississippi Kite nest trees have a larger dbh than randomly-selected trees (Table 3). Barber (1995) also reported the dbh of nest trees to be significantly larger than random trees. The large

dbh of nests trees may be correlated with age and size of the super-emergent trees typically used for nesting sites.

Mississippi Kites selected nest sites closer to the forest edge than random sites and all forest edges comprised of lakes, bayous, or the White River. This pattern was also documented during research previously conducted on the refuge (St. Pierre 2006). These bodies of water provide open areas for kites to forage for aerial insects. Barber (1995) reported kite nests were located closer to field edges more frequently than water edges. Field edges were uncommon within the interior of WRNWR, where waterways comprised the majority of the available edges. Whitmar (1987) reported kite nests in the Mississippi River Valley in Missouri had a mean distance to an edge of 49.2 m and a mean distance to water of 96.3 m. Edge habitats, particularly natural edges, seem to be an important attribute of Mississippi Kite nesting habitat.

Kite nests were more commonly built on secondary than on primary branches. Barber (1995) also documented this pattern for kite nests in Missouri and suggested this may be an anti-predator defense. Our data and those reported by Whitmar (1987) indicated kite nests were seemingly randomly placed throughout the nest tree.

CONSERVATION IMPLICATIONS

Mature tracts of forests should be conserved because this habitat type provides nesting sites and a foraging habitat for Mississippi Kites. Large, super-emergent trees should be conserved for kite nesting habitat. Management that promotes development of additional large, super-emergent trees will likely be beneficial to kites. Timber harvests consistent with kite conservation should be conducted so uneven-height canopy forests are created. We recommend that second-growth forest should be allowed to develop longer between harvests (>75 years) to provide foraging and nesting habitat for kites. Managers should avoid even-aged regeneration of clear-cuts and fallow fields. Natural waterways, including wetlands, should be conserved for production of prey and as foraging areas.

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BIOLOGICAL, GEOGRAPHICAL, AND CULTURAL ORIGINS OF THE LOON HUNTING TRADITION IN CARTERET COUNTY, NORTH CAROLINA

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ABSTRACT.—A tradition of shooting Common Loons (*Gavia immer*) for food and for bone fishing lures was established on Shackleford Banks, North Carolina, by the mid-19th century. This strongly ingrained tradition continued to be maintained, primarily by residents of nearby Harkers Island, when inhabitants of the banks moved inland about 1899. The practice probably arose because, on the east/west-tending Shackleford Banks, loons migrating northward in spring flew sufficiently low over land to be within shotgun range. Spring loon shooting, although illegal since 1918, grew to the point that dozens of hunters might be present on the banks on a given day. A strict law enforcement crackdown on this activity began in 1950, and the banks were effectively shut down for loon shooting. Loons continued to be shot opportunistically nearby, but a growing cultural intolerance of this practice brought the loon hunting tradition to an end. We document the existing memories and the few, scattered written sources concerning this unique local interaction between humans and birds. *Received 30 March 2010. Accepted 23 June 2010.*

On 6 May 1950, eleven federal and state wildlife enforcement officers staged a long planned, coordinated raid on Shackleford Banks, Carteret County, North Carolina, apprehending nearly 100 hunters, of whom 78 were formally charged with illegally shooting loons (Anonymous 1950) in violation of the Migratory Bird Treaty Act of 1918. This locally notorious event marked both the apogee and the rapid demise of a demographically narrow but strongly ingrained regional tradition, dating to the previous century, in which loons were hunted both for food and for use of their bones in making fishing lures. Loons do not usually factor so directly in human economy, nor does a similar loon hunting tradition seem to have evolved elsewhere, so we investigated whether some unique combination of biological and physiographical conditions may have given rise to the loon hunting tradition in Carteret County. We also attempted to document through interviews and published and unpublished local records, how the values and attitudes of one small community were molded by the perception of loons as an exploitable natural resource. The Carteret County loon hunting tradition has essentially been eradicated because of changes in the economic, legal, and ethical environment. Knowledge of this aspect of regional wildlife heritage is in danger of vanishing, hence the importance of its historical documentation.

METHODS

We interviewed residents of Carteret County, North Carolina, who had participated in loon hunting, or who had firsthand knowledge of some aspect of the circumstances under which loons were obtained or were directly employed for human use. We gathered numerous other sources that, although published, are of a very restricted or evanescent nature and mostly unavailable in major research libraries. These publications are held in the libraries of the Carteret County Historical Society, Morehead City, NC, and the Core Sound Waterfowl Museum and Heritage Center, Harkers Island, NC; photocopies of pertinent portions, as well as all of our interview notes, have been filed in the Smithsonian Institution Archives, Washington, D.C.

GEOGRAPHICAL CONSIDERATIONS

The key component of this story is a physiographical feature, Shackleford Banks, a long, 13.8 km (8.6 mi), narrow, barrier island with its northern shore separated from Harkers Island by Back Sound and whose southern shore is washed by the open Atlantic (Fig. 1). Unlike most Atlantic barrier islands that tend to run north to south, Shackleford Banks is oriented nearly east to west. The eastern end of the island is sheltered by Cape Lookout and lies somewhat farther south than the western end. This east/west orientation is of great significance when considering the spring migratory pathway of loons.

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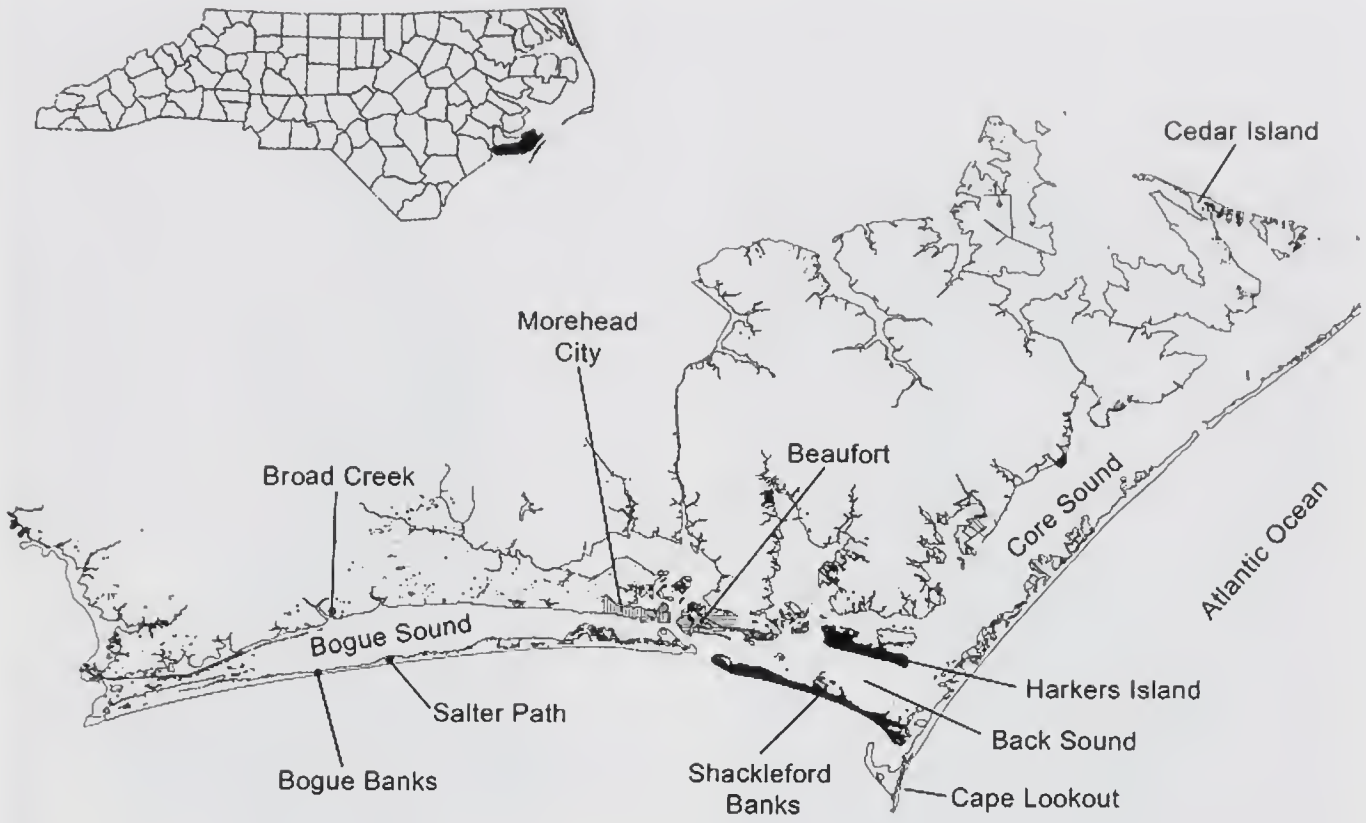

FIG. 1. Outline map of Carteret County, North Carolina, USA, showing localities mentioned in the text. Black emphasizes islands of particular importance in the history of loon hunting. Inset: Carteret County (in black) in relation to other counties of North Carolina.

Shackleford Banks was settled by the early 1700s and later came to have a considerable human population concentrated in two communities, Diamond City and Wade's Shore (or Wade's Hammock), whose inhabitants were mainly shore whalers who supplemented their livelihoods taking mullet (striped mullet *Mugil cephalus*) and porpoises (bottle-nosed dolphin *Tursiops truncatus*). A growing tendency for people to move off the banks to areas closer to commerce and other amenities was greatly accelerated in the late 19th century when the settlements were devastated, and Diamond City's high protective sand dune eroded away, by the great San Ciriaco hurricane that hit the outer banks on 17 August 1899. With the realization that the banks no longer provided a secure place to live, the Shacklefordians migrated inland, settling as far west as Salter Path on Bogue Banks, in the "Promise' Land" section of Morehead City, and to the northeast as far as Cedar Island. The majority, however, retreated to Harkers Island. Shackleford Banks was essentially uninhabited by 1902 and was used mainly as pasturage for hooved stock for most of the 20th century. Much of the preceding was summarized from Stick (1958). Shackleford Banks became part of the Cape Lookout National Seashore in 1966 (Public Law 89-366).

LOON BIOLOGY AND BEHAVIOR AS PERTAINS TO HUNTING

The Common Loon (*Gavia immer*) is a large, fish-eating waterbird that breeds on fresh-water lakes of boreal forests across North America and winters at sea along both coasts as far south as Mexico. It is a heavy bird with males reaching a maximum of 7.6 kg (16.8 lbs) and averaging almost 6 kg (13 lbs), with females averaging 4.7 kg (10.3 lbs) (Evers et al. 2010). There is considerable variation in weight (Evers et al. 2010), but spring migrants would probably seldom weigh much less than 4.5 kg (10 lbs). Loons probably were taken opportunistically for food in any subsistence culture, but they were seldom included among game birds desired by North American commercial waterfowlers or sportsmen. Not only are loons difficult to hunt, but because they are fish-eaters, there is a perception that they would taste "fishy" and not be particularly desirable for the table, much as fish-eating mergansers (*Mergus*) are generally disdained.

Loons are foot-propelled diving birds that spend their entire lives at the surface of or

underneath the water, except when flying or incubating eggs. The Common Loon has a very high wing-loading and requires a long run across water to get airborne (Savile 1957, Evers et al. 2010). Common Loons do not experience an energetically costly wing molt on the lakes of their northern breeding areas, which freeze over soon after the young have fledged. Thus, molt is delayed until they arrive in coastal wintering areas where all flight feathers are molted simultaneously and the birds are flightless until the new feathers grow in (Woolfenden 1967). Loons are not only reluctant to fly at sea in winter because it is energetically costly, but for considerable periods of time they are incapable of flight. Loons are solitary or thinly distributed in winter and do not respond to decoys as do waterfowl. They also ride low on the surface of the water, making them a difficult target for hunters. Pursuit by boat, even rapid motorized craft, may be ineffectual because once a loon dives it is difficult to predict when and where it may briefly surface.

The shooting journal of George Henry Mackay (1929) exemplifies the difficulty of shooting loons under normal circumstances and their greater vulnerability during their northward flight in spring. Mackay was an avid hunter of waterfowl and shorebirds as well as an amateur ornithologist and conservationist who kept a detailed journal, including numbers of all species shot, of his hunting trips in New England from 1865 to 1922. Of the thousands of birds recorded in his diary, he shot only 22 loons, of which 19 were taken at West Island, Rhode Island, on dates spanning 13 to 25 April, when birds were evidently passing over land shortly after departing on their spring flight north.

In spring migration, loons fly northward either along the coast or overland (Evers et al. 2010), but once having left the water they gain altitude and fly far above shotgun range. Birds along most of the north/south-trending eastern Atlantic Coast reach such high altitudes over water, perhaps offshore out of sight of land, and are thus not susceptible to shooting.

Along Shackleford Banks, however, loons accumulate off the east/west running ocean shoreline in spring and take off directly over land where they can be intercepted by gunners. The original Shacklefordians took advantage of this flaw in the loons' usual immunity to put meat on their table. Harkers Island later became the focal point for the continuation of loon hunting because of its proximity to the banks and the greater number of former Shackleford residents there (Fig. 1).

Many of the same conditions apply to Bogue Banks. Residents of the settlement of Salter Path in particular were known for shooting and relishing loons (Stephens 1984, Dudley 1993). Likewise, banksmen who settled on the mainland at Broad Creek crossed the sound to Bogue Banks for morning loon shoots near what is now known as Emerald Isle (Stephens 1984). We were told, however, that more loons cross at Shackleford Banks than farther west and this may come from a preference of loons to continue their northward flight over the waters of Core Sound, rather than over land.

LOON HUNTING IN CARTERET COUNTY, NORTH CAROLINA

We constructed the following history from interviews with local residents conducted in 2008 through 2010, augmented by a few scattered, generally recondite published sources. Most respondents' personal recollections date to the 1940s and early 1950s. Exactly when the loon hunting tradition arose is unrecorded, but one respondent's father told him that it was established by at least the mid-1800s. That seems reasonable considering that the practice must have been in place well before the Shackleford diaspora following the hurricane of 1899, as also suggested by Guthrie (1950). On Harkers Island, according to Paul and Paul (1996:13), the "sport... has been a part of their lives since the earliest days on the Island." Guthrie (1993:31) considered it "a favorite sport... since the conception of 'Diamond City' over a hundred years ago."

Loon hunting occurred in spring, beginning in March but mostly in April through mid-May. The usual procedure was for hunters to depart Harkers Island before daylight and leave their boats on the protected inner shore of Shackleford Banks. They dispersed on foot across the dunes to points along the Atlantic beach (Fig. 2) to await the flight of loons coming off the ocean that usually began at first light. Hunts occurred spontaneously as there was no deliberate organization. The recollection of one resident of Harkers Island was that shooting began so regularly at daybreak that "it was as good an alarm clock as you could ask for" and that at one point during World War II the shooting sounded like an invasion. The loons flew at their lowest altitude early in the morning and attained greater heights as the day progressed.

FIG. 2. Harkers Island resident Otis C. Willis (b. November 1918, d. June 1996) with the results of a loon hunt in 1943. Barely visible in the background in the photograph on the left is the Cape Lookout lighthouse and two boats proceeding northward through "The Drain" or Barden Inlet, which was created during the hurricane of September 1933. Thus, the photograph was taken at the easternmost end of Shackleford Banks. This photograph was incorporated as a patch entitled "The Loon Hunt" (illustrated in Amspacher 2009:94) in a community quilt on display in the Core Sound Waterfowl Museum and Heritage Center, Harkers Island, North Carolina.

Wind direction had an effect on flights of loons. A northeast wind was favored for shooting because a head wind made it easier for loons to take off from the water and fly directly over the banks. A southwest tailwind would keep birds flying for a greater part of the day and was more advantageous for birds once airborne, but those birds would likely have had to take off farther out to sea and turn before crossing the banks.

We were told that certain hunters once sank barrels in the sand for concealment (or shelter?), but no blind was usually deemed necessary beyond perhaps crouching behind any convenient large object that might have washed ashore. Anti-submarine buoys that had broken loose were mentioned as one such object used during and immediately after WW II. At the height of the loon shooting, hunters spaced themselves so regularly along the beach that there was hardly a place a loon could cross the banks without being in range of someone's shotgun. At times hunters were forced to stand behind one another. Loons are large and tough, and heavy shot, usually #2 or #4, was used. Even experienced gunners could be foiled at times, as one former shooter remembered expending a box of 25 shotgun shells without bringing down a single loon, although he then bagged five with his next five shots.

The object was to shoot the birds so they would fall on the beach or in the dunes behind. Wounded birds that fell in the water might escape either by diving and swimming away, or, when dead, might float off if winds or currents did not bring them back to the beach. Birds were not field dressed and were taken back intact, which meant an arduous trek back over the island with a heavy

load. One respondent recalled a day, when he was too small to carry a gun, that he had accompanied his father and uncle to the banks on a morning when they shot and retrieved 18 loons. That was probably near the practical upper limit for two people to carry because 18 loons together would have weighed well over 90 kg (200 lbs). That day's take was transported to the boat dangling from a pole carried over the shoulders of the hunters, a common practice, save for one loon that the youngster dragged behind him. Later, on Harkers Island, the boy sold the birds for 50 cents apiece or whatever anyone would give him.

There was no fall loon shoot because birds would be flying high and sometimes at night when arriving from the north and crossing land. But once the local appetite for loons had been established, birds might be taken opportunistically, other than in spring, on the banks. One respondent told of becoming adept at shooting loons on the water with a pistol. Stephens (1984:124) reported that Bogue Islanders "used to go to the [Bogue] sound and firelight them in November," which would also involve shooting birds on the surface of the water, but in that case at night with aid of a lantern.

USES OF LOONS

Food.—The primary impetus for hunting loons was for food. For 19th century residents of Shackleford Banks who had survived a winter on salt fish, root crops, and such grits and flour as they may have received in trade for mullet and whale oil in the previous months, a loon represented a sizeable chunk of fresh meat as well as a welcome change in diet. Loons do not migrate north until well after most ducks and geese have left for breeding areas and the "hardy group of fisher-folk" on Harkers Island "would rather have a 'loon-in-the-pot' than the more popular goose, canvasback, or red-head duck" (Paul and Paul 1996:13–14). We made a point of asking whether cormorants (*Phalacrocorax*) were ever shot for food. It was admitted that a cormorant would probably be just as good to eat as a loon but they were not taken.

One of Stephens' (1984:124) sources said that "I love the skin the best in the world" and Dudley (1993:137), whose source may have been the same, mentions that the birds were sometimes "picked." The prospect of plucking a loon is daunting and would require a great amount of work, so that a person would really have to desire the skin to go to the effort. Fat is what gives any kind of meat most of its flavor and most of a loon's fat is either attached to the skin or sequestered among the viscera. A loon with the skin on would likely be much more fishy-tasting than one that had the skin and feathers removed, although Dudley (1993:137) condescendingly avers that "fishy taste [is] barely discernable to the natives [of Harkers Island and Salter Path]." By far the greater number of loons prepared for cooking were skinned and usually only the breast and thighs were consumed. We have been assured that the end result did not taste fishy.

We inquired about loons of an acquaintance who came originally from Cedar Island and who had returned to Carteret County in retirement. He related that he had never shot a loon but would know exactly what to do if someone gave him one, and he proceeded to describe the entire process from carcass to stew bowl. Jocularly known as "Harkers Island turkey" (Amspacher 1987:217), additional sources for loon recipes (e.g., Stephens 1984, Amspacher 1987) are basically similar. The meat is soaked in water with salt or baking soda, browned in fried-out salt pork, and stewed to a thick gravy with some combination of onions, potatoes, rutabagas, and cornmeal dumplings. The process, which was at times done outside in large iron pots, would usually take most of a day.

Fishing Lures.—A secondary, but once important use of loons, was for fishing lures made from the bones, which were used for trolling with handlines, mainly for bluefish (*Pomatomus saltatrix*) and Spanish mackerel (*Scomberomorus maculatus*). H. Loftin remembers that in the 1930s loon bone lures were almost the only ones used for trolling in the Beaufort area. In addition to bones from birds shot for food, during WWII when tankers along the east coast were being sunk by German U-boats, bones for lures also came from loons that died from spilled oil and were cast up on the beach.

Almost all of our sources, both oral and published (e.g., Dudley 1993:137, Guthrie 1993, Paul and Paul 1996) insist that leg bones were used for the fishing lures and it seems from the descriptions that the tibiotarsus (drumstick) was meant. The femur of a loon is extremely short and curved, and the tarsometatarsus (foot) is flat and solid, so that neither of those bones would have been useful. That wing bones were also used is evident from the report that: "Watermen also

FIG. 3. Bones (A, B) of Common Loon (*Gavia immer*) and trolling lures (C–E) made from loon bones. A: complete left tibiotarsus and fibula; B: complete right humerus; C, D: from Dudley (1993:136); E: from collection of Roy H. Lewis, Stacy, North Carolina (photograph by J. R. Humphrey). The notch in D is clearly from hook wear.

want the wing and leg bones of the loons. They bleach them in the sun and cut them into 2 ½-inch [63 mm] lengths for fishing lures. The hollow bones are sometimes the only lures that will catch bluefish or Spanish mackerel'' (Dudley 2001: 160). Furthermore, Dudley (2001:165), relates that ''in olden days the hunters sold the leg and wing bones to Cheek's Hardware in Morehead City for 10 cents a piece.'' The only loon bone lures that we have been able to trace (Fig. 3 C–E) were clearly not made from any leg bone. They are all simple, completely terete cylinders that can only have been made from the humerus, the upper wing bone (Fig. 3B). The bone was beveled at one or both ends and the only one we examined personally (Fig. 3E) appeared to have been pared down to a smaller diameter. These bone cylinders were wired to a hook and the wire was said to have been twisted at the leading end of the bone in such a way as to give it a movement under water that was attractive to fish. An elderly resident of Harkers Island who agreed to demonstrate how to make a lure from a loon bone protested that the leg bones presented to him were too small for the purpose, lending further support to the available evidence that it was the humerus that was fashioned into lures. It is possible that the tibiotarsus was also used, as its flattened proximal surfaces (Fig. 3A) would probably have imparted an erratic motion under water that might have been attractive to fish. Such a lure would have had thinner walls and been more subject to splitting than one made from a humerus, which may account for why none seems to have survived if they ever existed. The walls of the humerus of a loon are much heavier and denser than in any bone of a duck or goose, which, had they been used for lures, would probably not have lasted long before being broken.

Following the demise of loon hunting, the supply of loon bones was greatly diminished and following WW II, loon bone lures were replaced by metal spoons and other trolling devices. Loon bone lures have now nearly completely disappeared from tackle boxes and tool sheds of Harkers Islanders.

LORE AND LEGENDS OF LOONS IN CARTERET COUNTY

It is natural that an activity that was such an integral part of local traditions as loon hunting would be incorporated into local storytelling and literature. More or less apocryphal stories about loon hunting on Shackleford Banks are still in circulation and may be recognized in several variants. One involves a newcomer to the sport who was taken to the banks one morning and witnessed a loon flying parallel to the beach and having each hunter along the line shoot feathers out of it until it kept on flying off into the distance nearly nude, provoking the hope that it would freeze to death. A version of this is told by Paul and Paul (1996). As loons were normally shot flying over the island, not parallel to it, and loons are not prone to losing many feathers when shot, this is likely a carryover from some dove hunter's tale. A similar anecdote that may be related involves a champion skeet shooter being invited to try his prowess on the banks who utterly failed to bring down a loon. In contrast with those failures, another story concerns a hunter returning from the banks to Harkers Island with a large haul. He repaired to the local movie theater, where he knew a large portion of the population would be, and announced that he had a skiff full of loons if anybody wanted one. Whereupon, the

theater emptied as people made haste for the skiff to get their loon.

Shooting and eating loons has also been incorporated into local humor, such as the joke about the man who was arrested and confessed to having shot a "seagull." Before sentencing, the judge asked the defendant why he wanted to shoot a gull in the first place, and the answer was that if it was cooked right it was "nigh bout goods a loon" (Williamson 2009:44).

Even poetic inspiration has been invoked in loon lore. We were told by several residents of Harkers Island that they recalled a high school boy in the 1950s who had written what we were first told was a story but were later assured was a poem about loon hunting, but from the perspective of the loon. We have not been able to trace a copy of said poem but it must have been an evocative one for its existence to be recalled more than half a century later. A more concrete literary contribution to the subject is a mystery novel, *Shooting at Loons* (Maron 1994), set in Carteret County, in which the prediliction of certain Harkers Island fishermen to poach loons illegally and make a stew of them is mentioned more than once.

THE END OF THE LOON HUNTING TRADITION

It became illegal to take or possess loons in 1918 with the adoption of the Federal Migratory Bird Treaty Act. Knowledge and enforcement of the law would doubtless have been scant and sporadic at first and the hardship years of the Great Depression, followed by World War II, would have made a limited local penchant for loon meat seem like a paltry Federal offense. But afterwards the Shackleford loon hunt became a victim of its own success. Too many people were participating in the hunt and were being joined to some extent by "sportsmen" from "off," whose main interest in loons would have been in extending their season to be afield with a gun. This created an additional problem of birds left dead on the beach by shooters who did not share the locals' appetite for stewed loon. Such conspicuous illegal activity could no longer be ignored.

In the late 1940s an undercover wildlife agent settled on Harkers Island with his family, where he came to be trusted by local residents, who conversed with him about fishing and hunting, including loon shooting. It was later perceived that his main purpose on Harkers Island, however, had been to set up the inevitable raid on the Shackleford Banks loon shoot (e.g., Guthrie 1993), a perception that was reinforced by the fact that he left the island before or immediately after the raid. The raid occurred on Saturday, 6 May 1950, and was led by Robert Halstead, a Federal agent of the U.S. Fish and Wildlife Service, who was joined by "Andrew Jones, chief state game protector" and nine other state agents. Some 100 loon hunters were "rounded up," but only 78 were actually charged, of whom "approximately 70" were from Harkers Island. Fifty loons were seized as evidence and Jones "estimated that 200 more were killed." We were told that some 25 or 30 other hunters escaped, which does not seem unlikely given the low ratio of agents to hunters. One of our sources, a teenager at the time, was among the escapees. The agents estimated that hunters were scattered "150 feet [45.7 m] apart for a distance of almost two miles [3.2 km]" and fired from "2000 to 2500 shots" in the first 15 min after the first shot at 0430 hrs. The math does not add up but it is clear there was a lot of shooting by a lot of people on that day. Decades later, Halstead provided his somewhat dramatized recollection of that day, complete with a photograph of 10 of the agents (the 11th was presumably the photographer) with some of the confiscated loons (Dudley 2001:159–163) but we have taken all portions in quotes above from a more immediate source (Anonymous 1950).

Those hunters who were convicted in federal court were fined $25, which is equivalent to about $225 in 2009 dollars, an amount that would have made an impression on those who had to earn that $25 by their labors on the waters. One may imagine that $1,750 of the entire 1950 economy of Harkers Island had a much more severe impact than would be conveyed simply by converting that figure into its modern spending power.

In retrospect, the May 1950 raid was a great deterrent success for law enforcement. There may have been no particular stigma (in fact perhaps the opposite) for most of those apprehended as loon shooters in Carteret County, but the public could no longer be unaware that such activity was egregiously illegal. The enforcers kept up their vigilance on Shackleford Banks for the next 2–3 years, after which any semblance of the loon shoots of old was abandoned.

Loon shooting persisted and probably still goes on to a limited extent. Hunting on Shackleford

Banks required leaving one's boat on the sound side to hunt on the ocean side, and, as a federally protected reserve, shooting there became too risky. But the occasional loon would still be taken along the "island shore," meaning the south shore of Harkers Island. One such incident resulted in a falling loon hitting a power line on the way down and knocking out electricity for part of the island, which "did not go over" well among some of those in positions of authority at the time. Even after the law had come down hard in 1950, residents of Salter Path and elsewhere on Bogue Banks continued to "sneak to the beach hills and elsewhere in an attempt to get a loon.... Some of them didn't kill many the whole spring. But if they killed two or three, they divided them with their family connections. It was a big thing. They called in their sister or father or mother or something like that" and still do so "if they can get a hold of them" (Stephens 1984:124). Dudley (1993:137) reported that at "Salter Path, the hunters sat on high knolls or dunes anticipating loon flights over low-lying areas or swashes. With the pressure of development and high-rise condominiums, this practice has nearly ceased. Today, loon hunters position themselves around their homes, or wherever they can obtain visibility of loon flights, and the shooting continues. Gun shots are still heard, and game wardens still abound." Given the pace of development on Bogue Banks since that passage was written, the incidence of surreptitious loon shooting there has by now probably all but vanished.

EPILOGUE

An impassioned, even lyrical, paean evoking the emotions and near ritual importance of the loon hunt was printed in the *Carteret County News-Times* shortly after the great raid of May 1950 (Guthrie 1950). Guthrie contended that the laws that overregulated hunting had come into effect because of "fancy" "upstate" sportsmen, whereas the Carteret County loon shooters participated in the "only exciting sport left untouched by the law. Their father had done it, their grandfather before, even before their forefather had moved from the outer banks. You weren't a man until you had shot a loon." Hours before daylight, fathers would rouse sons too small to carry a gun from their beds to cross the sound to the banks and participate in the Harkers Island rites of spring. In the later days of shooting on the banks, "the excitement of the forbidden hunt [would add] zest to the sport" (Paul and Paul 1996:13). One of our respondents, now a pillar of the Harkers Island community, stirring up recollections over 60 years old, admitted that although he did not really know what it was like to be addicted to anything, he thought that he had been a loon hunting addict. The motivation was not the thought of a meal, it was the uniqueness of "the sport."

Old traditions die hard, but shooting and eating loons as part of the economy and culture of coastal Carteret County is now a nearly forgotten part of the past. The Common Loon has become the object of such romantic and mythical sentimentality in most of North America (Evers et al. 2010) that there could now be no tolerance for even a small unsanctioned harvest of this species. The day is not far away when no one on Harkers Island will recall the taste of stewed loon, just as there is almost no one alive who remembers how to fashion a trolling lure from a loon bone. This interesting and unique local tradition between humans and birds now exists almost only as a historical phenomenon that deserves to go on record.

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MIGRANT SONGBIRD SPECIES DISTRIBUTION AND HABITAT USE DURING STOPOVER ON TWO ISLANDS IN THE GULF OF MAINE

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ABSTRACT.—We compared the distribution of migrant bird species between two islands in the Gulf of Maine to examine if differences in habitat resulted in differences in avian species composition and relative abundance during stopover. Ninety-one species were captured on both islands and those species captured on only one island were either breeding species or rare visitors to the islands. Differences in bird species distribution between islands were species-specific and consistent among sampling periods for nearly all species. Twelve species were captured more frequently on Star Island and 11 species more frequently on Appledore Island. Stopover species distribution appeared to be related to habitat structure, vegetation, diet, and habitat area. Scrub-shrub/open habitat breeding species and forest breeding species were not evenly distributed between islands. Island use was most closely associated with breeding habitat. All but two of the eight species that breed in scrub-shrub or open habitat were captured more frequently on Star Island. Ten of the species more common on Appledore Island breed in forested habitat. Nine of the 11 species more common on Appledore Island are area-sensitive in breeding areas, suggesting potential area sensitivity during migration. Differential habitat use indicates a large number of stopover sites in a wide variety of habitats are necessary to meet migration needs of passerine species. *Received 17 November 2006. Accepted 22 April 2010.*

Suitable stopover habitat is critical to a successful migration (Moore et al. 1995) and loss of stopover habitat may be a factor in long-term population declines (Sherry and Holmes 1995, Finch and Wang 2000, Hutto 2000). Migrants have increased risk of mortality during migration (Bairlein 1992; Moore et al. 1992, 1995; Hutto 1998; Sillett and Holmes 2002.) without habitat that can satisfy their needs to replenish critical energy supplies, reorient (Baird and Nisbet 1960), escape adverse winds and weather, recover from muscle fatigue or injury, and avoid the dehydration of daytime flight. More information is needed on habitat requirements of passerines during migration (Moore et al. 1992, 1995; Sherry and Holmes 1995; Hutto 2000; Petit 2000) to understand what constitutes valuable stopover habitat and influences habitat selection (Moore et al. 1995, Dunn 2000).

Migrants show differential habitat use including species-specific distribution among stopover habitats (Hutto 1985, Moore et al. 1990, Winker 1995), but the basis for habitat selection is not clear. Finch and Wang (2000) reported bird densities during migration were affected by vegetation structure and habitat type, but few studies have examined fine-scale habitat relationships during migration (Rodewald and Brittingham 2004). There is some evidence that songbirds may select stopover habitat with vegetative characteristics similar to their breeding habitat (Parnell 1969, Petit 2000). Other factors affecting stopover habitat use may include suitability to a species' foraging method (Bairlein 1992), food availability (Hutto 1985, Moore et al. 1995), dietary shifts (Parrish 2000), predation and competition (Moore et al. 1992), and site characteristics including area (Moore et al. 1995), temperature, and humidity (Winker 1995).

Star and Appledore islands are part of the Isles of Shoals on the New England coast, USA. They provide a unique opportunity to examine the relationship between habitat and migrant stopover patterns because large numbers of songbirds stop at the archipelago during spring and fall migrations (Morris et al. 1994, 1996), and the islands are <1 km apart. Weather and body mass can influence selection of stopover sites (Moore and Simons 1992) and the potential confounding effect that different weather conditions have on migration behavior can be eliminated by comparing two adjacent sites. Both islands are categorized as maritime shrub thicket (Sperduto and Nichols 2004), which encompasses a range from low-growing shrubs to tall thickets; comparison of these islands presents an opportunity to examine the relationship of birds and stopover habitat at a fine scale. Species richness and abundance in

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migration may be correlated with patch size (Martin 1980, Blake 1986, Somershoe and Chandler 2004), as has been shown during the breeding season when number of species and individuals increases with area (Freemark and Merriam 1986, Blake and Karr 1987, Faaborg et al. 1995). Star Island is smaller than Appledore Island allowing consideration of area effects on species composition during stopovers.

Our objectives were to examine: (1) whether there were differences in species richness, composition, and distribution between the islands; and (2) whether a species' breeding habitat or food habits were related to stopover habitat use. We predicted more species would be captured on Appledore Island and that habitat differences between islands would result in differences in species composition and frequency of capture.

METHODS

Study Site.—The Isles of Shoals is a group of nine small islands and several ledges in the Gulf of Maine, 14.5 km southeast of Portsmouth, New Hampshire (42° 58′ N, 70° 36′ W), and 9.7 km from the nearest point of the mainland. Appledore Island, Maine is the largest of the islands at 33.6 ha and Star Island, New Hampshire is 13.4 ha. The minimum shore-to-shore distance between Star and Appledore islands is ~0.7 km and the study sites were 1.6 km apart.

Bird Surveys.—Bird surveys were conducted simultaneously on both islands in 1999 and 2000 using mist nets during spring and fall migration following the protocol established for the Appledore Island Migration Banding Station (Morris et al. 1994, 1996). There were four sampling periods: 11 May–8 June 1999, 10 May–8 June 2000, and 16 August–30 September 1999 and 2000. Weather permitting, mist nets (6 or 12 × 2.6 m, 4 shelves, 30 mm mesh) were operated during daylight hours with the nets opened just before sunrise, closed at sunset, and checked every 30 min throughout the day. Up to five nets were operated on Star Island and up to 10 nets were operated on Appledore Island. Captured birds were brought to a central location on each island and banded with USGS aluminum bands.

Habitat Surveys.—We collected habitat data at net sites rather than at random locations distributed over each entire island. There is extreme landscape variability on both islands with habitat ranging from rocky splash zones or mowed lawns to thick scrub-shrub relatively close to the nets. We characterized the natural vegetation that surrounded the mist nets to ensure data were representative of the habitat used by the species captured. These data should not be considered representative of the habitat on the entire island.

Vegetative structure and composition at each site were measured using a modified version of James and Shugart (1970) and Winker et al. (1992). We established eight circular survey plots, each centered on a pair of mist nets (or a single net, if there was only one in a given area). There were three plots on Star Island and five on Appledore Island covering all net locations. Each plot was 0.04 ha (radius = 11.35 m) and was divided into two semicircles, separated by the net lane (1–2 m) to remove the non-vegetated lane from analysis.

We established six 1.5 m-diameter circular subplots in each plot using a stratified random design so each subplot was entirely within the larger plot. Subplots were located by extending a random distance into alternating halves of the plot from six equidistant points (3.94 m apart) along the diameter of the plot, excluding the outer 1.5 m. We established a 1 m-wide transect in each half of the plot to measure shrub density. Transects were parallel to the net lane and 0.3 m from the edge of the net lane to reduce the influence of trimming along net lanes.

We defined trees as woody stems with a diameter at breast height (dbh) $\geq$3.0 cm and shrubs as any woody vegetation $<$3.0 cm dbh and over 0.75 m in height. We recorded live tree species, height, and dbh (0.1-cm diameter tape) in each plot. We recorded only dbh for dead trees. We recorded species and height for each live shrub stem in the transect, and counted stems separately if they branched within 0.1–0.2 m above the ground. We counted the number of stems for dead shrubs. Heights for live trees and shrubs were measured to the nearest 0.1 m. Separate measurements were taken for each species in a cluster.

We measured herbaceous cover, canopy cover, and vegetation density in each subplot. We visually estimated herbaceous cover in each subplot to the nearest 5%. We visually estimated canopy cover from the center of each subplot and recorded cover to the nearest 5% at six 1-m height classes beginning with 0–1.0 m (to account for low woody plant cover that functions as canopy for ground-feeding birds). We used a density board (Nudds 1977) placed at the center of a

subplot to measure vegetation density and estimated percent cover from 2 m distant, rather than the recommended 15 m (Nudds 1977), because of the extreme density of the shrub vegetation. We chose a random direction using eight possible points of the compass and rejected points that were outside the full plot after walking 2 m from the board. We recorded vegetation cover to the nearest 5% in each of the four sections of the density board (0–0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0 m).

All habitat data were collected between 6 May and 10 June 2000 by RWS to eliminate variability among observers. Subplot measurements were obtained between 5 and 10 June to ensure that vegetation density and canopy cover measurements were at the same time after leaf out.

Data Analysis.—We used Systat Version 10 (SPSS Inc. 2000) for statistical analyses. The analyses, except bird species richness, include only those species that do not breed on the Isles of Shoals (i.e., only stopover migrants). We used raw counts of birds captured for all Chi-square tests.

We used a heterogeneity Chi-square analysis (Zar 1999) to test for differences in species distribution between islands and analyzed each sampling period separately. We used Freeman-Tukey deviates in Systat to examine which species were responsible for significant Chi-square tests. We removed those species from the analysis until there was no difference ($P > 0.05$) between islands. Expected values for individual species were calculated using the total number of migrant birds captured on each island. The heterogeneity test was the prime analysis used in examining differences between islands, even though expected values for some species were below the desired criteria for Chi-square tests. We used a Chi-square goodness-of-fit test for each species as a secondary analysis to compare number of individuals captured between islands without violating the expected value criteria. Expected values were ≥5 in all tests except Purple Finch (*Carpodacus purpureus*) and Savannah Sparrow (*Passerculus sandwichensis*) in spring 2000.

We followed Jones et al. (2002) and the recommendations of Gotelli and Ellison (2004), and did not use Bonferroni corrections in the analyses to reduce the likelihood that real differences or relevant patterns would be missed. Bonferroni corrections are not as practical for diverse communities requiring multiple statistical tests (Moran 2003) such as the number of migrant birds in this study. It is unlikely the results from all tests will be spurious (Moran 2003).

Species were included in the distribution analysis if there were ≥10 individuals banded on at least one island in any two sampling periods, and were analyzed in only those sampling periods when their numbers met this minimum criterion. The only exception was Purple Finch, which is an irruptive migrant present in large numbers during fall 1999 only. We included it in the spring 2000 analysis, although only eight individuals were banded, to examine if the return migration in spring had the same distributional pattern. Recaptures were not included in the distribution analysis.

We used a Mann-Whitney *U*-test to compare mean number of tree and shrub stems per plot between islands for each species with more than 20 stems on one of the islands. We computed the mean per plot for each island and compared means between islands using a Mann-Whitney *U*-test for the habitat data: live tree and shrub density (all species combined), dead tree and shrub density, tree and shrub height, and tree dbh. A mean for each individual plot was calculated first for the latter three measures, which were used to calculate the mean per plot for the entire island. We divided tree heights into five 1-m height classes beginning with 2.0 m and shrub heights into five 0.5-m height classes beginning with 0.5 m. We compared the distribution of trees and shrubs by height class between islands with a heterogeneity Chi-square analysis, and used a Mann-Whitney *U*-test to examine differences among mean number of stems per plot in each height class. We divided tree dbh into seven size classes: 3–3.9, 4–4.9, 5–5.9, 6–6.9, 7–10.9, 11–15.9, and ≥16.0 cm. The larger size classes with few trees were combined to create suitably sized groupings. We compared the distribution of trees by dbh class between islands with a heterogeneity Chi-square analysis. We used ANOVA to compare percent herbaceous cover between islands and MANOVA with associated univariate tests, when the MANOVA was significant, to compare mean vegetation density at four height classes and canopy cover at six height classes between islands.

We assigned habitat types to each bird species for breeding habitat to compare species differences between islands with habitat associations in breeding areas. Habitat classifications were: early successional, forest, forest edge, low forests at high elevations and in bogs, scrub-shrub, and open areas (including grasslands and emergent wet-

lands). We also examined vegetation type and area sensitivity in breeding areas. Area sensitivity information was obtained from Robbins et al. (1989) and Birds of North America species accounts (Poole and Gill 1993–1997, 1998–2002); breeding habitat information was primarily from DeGraaf and Yamasaki (2001) supplemented by Ehrlich et al. (1988). We classified fall frugivory into four categories using the mean percent of fruit in fecal samples during fall migration on Block Island, Rhode Island (Parrish 1997): low 0–29, medium 30–59, medium-high 60–89, and high 90–100%.

RESULTS

Bird Species Richness.—We banded 5,443 birds (3,833 migrants) on Star Island and 8,372 (6,604 migrants) on Appledore Island during the four sampling periods. Mean (± SD) captures for Star Island were 1,234 ± 28.3 in spring and 1,487 ± 255.3 in fall, and for Appledore Island were 2,140 ± 302.6 in spring and 2,046 ± 233.3 in fall. Ninety-nine species were captured on Star Island and 102 on Appledore Island; 91 of the species were captured on both islands. Mean (± SD) species richness for all sampling periods combined was 68 ± 4.65 for Star Island and 74 ± 3.16 for Appledore Island. Mean (± SD) species richness during spring was 64 ± 0.71 on Star Island and 71 ± 0.71 on Appledore Island; during fall it was 72 ± 0.71 on Star Island and 76 ± 2.12 on Appledore Island.

Eight species were captured only on Star Island and 11 species only on Appledore Island. Some species were captured infrequently and were rare visitors to the Isles of Shoals or unusual captures in songbird mist nets. More of these "accidental" species would be expected on Appledore Island due to probability (more net hours). Species richness on the two islands was identical at 70 species with 100% overlap in species composition between the islands when we removed breeding and accidental species from the analysis.

Bird Species Distribution.—The distribution of migrant species between islands differed in each sampling period (spring 1999: $\chi^2 = 242.27$, df = 28, $P \leq 0.001$; spring 2000: $\chi^2 = 206.19$, df = 33, $P \leq 0.001$; fall 1999: $\chi^2 = 325.92$, df = 31, $P \leq 0.001$; fall 2000: $\chi^2 = 400.69$, df = 34, $P \leq 0.001$). The difference between islands was attributed to a fairly consistent group of species (Table 1). Twelve species were captured more frequently than expected on Star Island (scientific names in Table 1): Traill's Flycatcher, Ruby-crowned Kinglet, Cedar Waxwing, Magnolia Warbler, Yellow-rumped Warbler, Wilson's Warbler, Yellow-breasted Chat (fall, not tested in spring), Savannah Sparrow (spring, not tested in fall), Lincoln's Sparrow (fall but not spring), Swamp Sparrow, White-throated Sparrow (fall but not spring), and Purple Finch. Eleven species were captured more frequently than expected on Appledore Island (Table 1): Red-eyed Vireo, Brown Creeper (fall, not tested in spring), Veery (fall but not spring), Swainson's Thrush (spring but not fall), Black-throated Blue Warbler, Black-and-white Warbler, American Redstart (fall but not spring), Ovenbird, Northern Waterthrush, Mourning Warbler (spring but not fall), and Canada Warbler (spring but not fall).

Habitat.—Thirteen species of shrubs and eight species of trees were recorded on Star Island and 15 species of shrubs and nine species of trees on Appledore Island (Table 2). The most common shrub species in the netting area on Star Island were chokeberry, raspberry, and rose; the most common trees were winterberry, sumac, and bayberry (scientific names in Table 2). The most common shrubs in the netting area on Appledore Island were chokecherry, winterberry, and arrowwood; the most common trees were chokecherry, serviceberry, and arrowwood. Only raspberry and winterberry were in the top five species on both islands; the other dominant species were typically scarce or absent on the other island. Bayberry and huckleberry were recorded only on Star Island, and apple, arrowwood, black cherry, and pin cherry were recorded only on Appledore Island.

The mean number of trees on Appledore Island was higher than on Star Island, but this difference was not significant for all heights combined (Table 3). One Star Island plot had 228 trees, but the mean of the two remaining plots was only 65 trees. No plot on Appledore Island had <142 trees. The distribution of trees over five height classes differed ($\chi^2 = 375.5$, df = 4, $P \leq 0.001$) between islands (Fig. 1). Appledore Island had more trees per plot in the highest three classes and Star Island had more in the lowest class. The difference between islands was not significant for the 3–3.9 m height class. There were also fewer dead trees per plot on Star Island than Appledore Island (Table 3).

Trees on Star Island had a smaller mean dbh per plot (range = 3.0–10.7 cm) than Appledore Island (range = 3.0–33.2 cm; Table 3). The distribution

of trees over seven dbh classes differed (χ^2 = 50.6, df = 6, $P \leq 0.001$) between islands with fewer trees on Star Island in all dbh classes, and fewer than 10 trees in the four classes greater than 6.0 cm. Star Island had shorter mean tree height per plot than Appledore Island (Table 3). There were only six trees taller than 4.0 m on Star Island (3 plots), whereas Appledore Island had 529 that were 4.0 m or taller (5 plots).

Shrub density was higher on Star Island than Appledore Island, primarily because of a difference in the number of small-diameter shrubs (Table 3). Star Island had more dead shrubs per plot than Appledore Island but the difference was not significant (Table 3). Overall mean shrub height did not differ between islands (Table 3). However, distribution of shrubs over five height classes (Fig. 1) differed (χ^2 = 729.5, df = 4, $P \leq 0.001$) between islands. Star Island had significantly more shrubs per plot in the lowest three classes and Appledore had significantly more in the highest height class. There was no difference (P = 0.881) between islands in the 2–2.4 m class.

There was a slight difference between islands in vegetation density for all four heights combined ($F_{4,43}$ = 2.48, P = 0.058). Star Island had significantly higher mean percent cover than Appledore Island in the lowest two height classes (0–0.5 and 0.5–1.0 m) but there was no significant difference in the two upper heights.

Percent canopy cover differed ($F_{6,41}$ = 4.25, P = 0.002) between islands. Star Island had higher percent cover in the lowest two height classes from 0.0 to 2.0 m, and Appledore Island had higher percent cover in the highest three classes (3.1 m and higher); one height class (2.1–3.0 m) did not differ between islands. Star Island had mean (± SD) herbaceous cover of 52.5 ± 34.2% and Appledore Island had a mean cover of 35.8 ± 35.0%, but the difference was not significant ($F_{1,46}$ = 2.69, P = 0.112).

Comparison of Bird Distribution with Habitat.—There were fewer trees on Star Island and they were smaller in height and dbh than Appledore Island which had only six trees taller than 4.0 m (3 plots), whereas Appledore Island had 529 that were 4.0 m or taller (5 plots). Star Island had more shrubs in all height classes except the tallest (>2.5 m), and had the highest vegetation density in all height classes except the highest (1.5–2.0 m). Appledore Island had more canopy cover except in the 0–2.0 m range. Thus, Star Island more closely resembled a typical scrub-shrub habitat in structure while taller thickets with higher canopy cover characterized Appledore Island. This difference allowed us to compare differences in bird distribution between islands in relation to habitat (Table 4).

There were significant differences in distribution between islands (χ^2 = 4.5, df = 1, P = 0.033) when bird species were grouped based on breeding habitat as (1) scrub-shrub or open, or (2) forest. Six of the eight species that breed in scrub-shrub or open habitat were captured significantly more frequently on Star Island (Table 4); one of the other two showed no difference between islands (Chestnut-sided Warbler) and the other was more numerous on Appledore Island (Mourning Warbler). Six of 32 forest-breeding species were more common on Star Island, 10 were more common on Appledore Island, and 16 showed no difference between islands (Table 4). Nine of 12 forest-breeding species that are area-sensitive in breeding areas were more common on Appledore Island, and the other three species showed no difference between islands (Table 4).

DISCUSSION

Star Island more closely resembled a typical scrub-shrub habitat in structure with denser shrub vegetation, more trees, and greater canopy cover <3.0 m. Appledore Island had greater tree density, canopy cover, and shrub density >3.0 m. Bird species richness and composition varied minimally between islands; however, relative abundance of some species varied greatly probably because of vegetation differences. These results are consistent with Rodewald and Brittingham (2004) who reported relative abundance during migration varied among habitats despite broad habitat use by all species.

Differences in species distribution between Star and Appledore islands were species-specific and consistent between sampling periods. Bairlein (1983) and Moore et al. (1990) also reported high consistency of species-specific habitat distributions and that migrants show selective use of certain habitats. There was no consistent relationship to winter habitat but there was to breeding habitat.

Most migrant species that breed in scrub-shrub and open habitat were more numerous on Star Island, except for Chestnut-sided and Mourning warblers. The shorter vegetation on Star Island

TABLE 1. Bird species distribution between Star Island (SI) and Appledore Island (AP) based on banding data from 1999 and 2000. H/g = Chi-square heterogeneity and goodness-of-fit analyses; H = species responsible for the difference between islands. A — indicates no difference between the islands and blank = capture numbers insufficient for analysis in that sampling period. Island = location where relatively more of that species were captured.

		Spring							Fall						
		1999			2000				1999			2000			
Species	Scientific name	SI	AP	H/g	SI	AP	H/g	Island	SI	AP	H/g	SI	AP	H/g	Island
Northern Flicker	*Colaptes auratus*	1	2		0	2			19	43	−/−	8	17	−/−	—
Eastern Wood-Pewee	*Contopus virens*	14	38	−/−	25	38	−/−	—	5	6		11	20	−/−	—
Yellow-bellied Flycatcher	*Empidonax flaviventris*	8	27	−/−	29	48	−/−	—	6	20	−/g+	19	44	−/g+	—
Traill's Flycatcher	*E. traillii/alnorum*	32	25	H/g**	50	50	H/g**	SI	18	15	H/g+	34	34	—	SI
Least Flycatcher	*E. minimus*	5	9		24	40	−/−	—	6	25	−/g*	35	22	H/g**	Both
Eastern Phoebe	*Sayornis phoebe*	0	1		0	0			12	20	−/−	5	11	−/−	—
Blue-headed Vireo	*Vireo solitarius*	6	23	−/−	6	28	−/g*	AP	9	21	−/−	19	10	H/g**	SI
Philadelphia Vireo	*V. philadelphicus*	0	0		1	6			6	14	−/−	17	32	−/−	—
Red-eyed Vireo	*V. olivaceus*	26	156	H/g**	62	164	H/g**	AP	69	230	H/g**	116	354	H/g**	AP
Red-breasted Nuthatch	*Sitta canadensis*	5	7		4	10	−/−	—	32	94	−/ g**	0	2		—
Brown Creeper	*Certhia americana*	1	0		0	0			5	33	H/g**	4	16	H/g+	AP
Golden-crowned Kinglet	*Regulus satrapa*	0	0		1	1			14	26	−/−	71	94	−/−	—
Ruby-crowned Kinglet	*R. calendula*	47	28	H/g**	16	5	H/ g**	SI	9	21	−/−	40	37	−/g*	(SI)
Veery	*Catharus fuscescens*	4	12	−/−	5	10	−/−	—	2	10	−/−	4	17	H/g*	AP
Swainson's Thrush	*C. ustulatus*	2	33	H/ g**	13	40	−/g+	AP	6	14	−/−	5	15	−/−	—
Cedar Waxwing	*Bombycilla cedrorum*	10	7	H/g**	26	14	H/g**	SI	56	70	H/−	76	50	H/g**	SI
Nashville Warbler	*Vermivora ruficapilla*	7	12	−/−	11	18	−/−	—	10	9	−/−	32	52	−/−	—
Northern Parula	*Parula americana*	24	103	−/g*	14	33	−/−	—	11	12	−/−	13	8	−/g*	—
Chestnut-sided Warbler	*Dendroica pensylvanica*	16	33	−/−	17	17	−/g*	—	1	9		8	16	−/−	—
Magnolia Warbler	*D. magnolia*	137	258	H/g*	159	254	−/−	SI	23	24	H/−	57	61	−/g+	SI
Black-throated Blue Warbler	*D. caerulescens*	16	74	−/g*	7	25	−/g+	AP	15	53	−/g**	11	53	H/g**	AP
Yellow-rumped Warbler	*D. coronata*	20	14	H/g**	30	12	H/g**	SI	199	47	H/g**	145	20	H/g**	SI
Black-throated Green Warbler	*D. virens*	11	19	−/−	13	12	−/−	—	7	8		12	17	−/−	—
Blackburnian Warbler	*D. fusca*	5	13	−/−	16	16	−/−	—	2	1		3	3		
Blackpoll Warbler	*D. striata*	27	106	−/g+	51	88	−/−	—	45	75	—	29	27	−/g+	—
Black-and-white Warbler	*Mniotilta varia*	18	72	−/g+	10	56	H/g**	AP	14	45	−/g*	33	93	H/g**	AP
American Redstart	*Setophaga ruticilla*	42	138	−/−	67	133	−/−	—	34	96	−/g**	85	208	H/g**	AP
Ovenbird	*Seiurus aurocapilla*	7	112	H/g**	10	59	H/g**	AP	2	21	H/g**	7	35	H/g**	AP
Northern Waterthrush	*S. noveboracensis*	10	57	−/g*	8	39	H/g**	AP	66	133	−/g+	100	228	H/g**	AP
Mourning Warbler	*Oporornis philadephia*	9	17	−/−	6	29	H/g*	AP	10	10	−/−	13	18	−/−	—
Wilson's Warbler	*Wilsonia pusilla*	12	11	H/g*	38	18	H/g**	SI	18	20	H/−	53	37	H/g**	SI
Canada Warbler	*W. canadensis*	12	34	−/−	9	60	H/g**	AP	1	5		13	31	−/−	—

TABLE 1. Continued.

Species	Scientific name	Spring							Fall					
		1999			2000				1999			2000		
		SI	AP	H/g	SI	AP	H/g	Island	SI	AP	H/g	SI	AP	H/g	Island
Yellow-breasted Chat	*Icteria virens*	0	0		0	1			31	24	H/g*	28	7	H/g**	SI
Savannah Sparrow	*Passerculus sandwichensis*	13	6	H/g**	10	1	H/g**	SI	2	0		0	0		
Lincoln's Sparrow	*Melospiza lincolnii*	2	9		21	28	−/−	—	11	2	H/g**	10	3	H/g**	SI
Swamp Sparrow	*M. georgiana*	45	31	H/g**	26	17	H/g**	SI	7	2		17	4	H/g**	SI
White-throated Sparrow	*Zonotrichia albicollis*	39	70	−/−	29	63	−/−	—	95	119	H/−	28	26	−/g+	SI
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	3	16	−/−	9	25	−/−	—	6	2		6	3		
Baltimore Oriole	*Icterus galbula*	4	9		8	12	−/−	—	17	25	−/−	19	30	−/−	—
Purple Finch	*Carpodacus purpureus*	0	0		8	2	H/g**	SI	42	31	H/g**	0	0		SI

+ = $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and − = differences not significant.

with its greater density at lower heights and scarcity of taller trees may be more suitable for scrub-shrub species than Appledore Island. Bairlein (1983) also reported differences in species along a gradient of vegetation density, and Rodewald and Brittingham (2004) reported shrub-sapling breeding species were most abundant in early successional and edge habitat during fall stopover.

Ten of the 11 migrant species captured significantly more frequently on Appledore Island breed in forested habitat with the exception being Mourning Warbler. However, not all forest-breeding species were more numerous on Appledore Island. Nine of the 10 forest-breeding species that were more numerous on Appledore Island are area-sensitive in breeding areas. No area-sensitive species was more numerous on Star Island. Other studies have reported evidence of area-sensitivity during migration (Martin 1980, Cox 1988, Somershoe and Chandler 2004). The influence of patch size on stopover habitat use is also influenced by microhabitat and landscape (Petit 2000). The influence of habitat area in our study was not reliably separated from habitat structure. For example, area-sensitive species may be less flexible in migration stopover habitat than other forest breeding species and, thus, more common on Appledore Island because of its more forest-like habitat.

Microhabitat factors likely contributed to the distribution patterns of forest-breeding species. American Redstart breed in habitat with a dense sapling (2.5–9.9 cm dbh) understory (DeGraaf and Yamasaki 2001). Appledore Island had far more trees in this size class than Star Island. Appledore Island also had more and larger trees than Star Island. Black-and-white Warblers were recorded only on large limbs of larger trees during spring migration in Kentucky (Mason 1979) and were more common on Appledore Island. Brown Creeper was the only forest-breeding species more common on Appledore Island that is not area-sensitive. It forages primarily on large-diameter trees with deeply furrowed bark (Hejl et al. 2002). This feeding substrate is almost totally lacking on Star Island but is present on Appledore Island.

Fruit availability also seemed to affect the distribution of species. Three of the six species more numerous on Star Island that were not scrub-shrub or open habitat breeders appeared to be influenced by presence of fruit-bearing shrubs.

TABLE 2. Tree and shrub species composition on Star and Appledore islands sampling plots (0.04 ha) in 2000. Differences in means based on Mann-Whitney *U*-tests for between islands. A — indicates insufficient numbers for analysis (20 or fewer stems). Species with <10 stems (total trees and shrubs combined) on both islands were not analyzed[c].

Common name	Scientific name	Star Island		Appledore Island		Difference	
		Shrubs	Trees	Shrubs	Trees		
		Mean per plot	Mean per plot	Mean per plot	Mean per plot	shrubs	trees
Apple	*Pyrus malus*	—	—	0.6	4.0		
Arrowwood	*Viburnum recognitum*	—	—	56.0	23.6	+	+
Northern bayberry	*Myrica pensylvanica*	35.3	12.0	—	—	+	+
Blackberry	*Rubus allegheniensis*	12.3	—	9.4	—	−	
Black cherry	*Prunus serotina*	—	—	—	10.0		*
Chokeberry[a]	*Pyrus* spp.[a]	430.7	—	0.8	—	*	
Chokecherry	*Prunus virginiana*	3.3	9.0	87.8	55.0	*	*
Huckleberry	*Gaylussacia baccata*	11.3	—	—	—	−	
Pin cherry	*Pyrus pensylvanica*	—	—	2.8	11.8		−
Poison ivy	*Toxicodendron radicans*	19.0	1.0	—	0.4	+	
Raspberry	*Rubus ideaus*	296.0	—	30.2	—	−	
Rose[b]	*Rosa* spp.[b]	158.0	—	13.4	—	*	
Serviceberry	*Amelanchier* spp.	1.0	6.7	2.0	46.6		*
Staghorn sumac	*Rhus typhina*	1.0	19.3	5.4	9.6	−	−
Winterberry	*Ilex verticillata*	76.3	68.3	57.2	36.2	−	−

+ = $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and − = differences not significant.
[a] Red and purple chokeberry (*P. arbutifolia*, *P. floribunda*) and possible hybrids.
[b] Virginia rose (*R. virginiana*) on both islands, pasture rose (*R. carolina*) only on Appledore Island.
[c] Species with fewer than 10 stems: carrion-flower (*Smilax herbacea*), common elder (*Sambucus canadensis*), bittersweet nightshade (*Solanum dulcamara*), red cedar (*Juniperus virginiana*), red maple (*Acer rubrum*), Virginia creeper (*Parthenocissus quinquefolia*).

The Yellow-rumped Warbler feeds on bayberry during fall migration (Parrish 1997); this shrub was moderately common on Star Island but absent from the Appledore Island plots. The other two species, Cedar Waxwing and Purple Finch, were two of the four highly frugivorous species present in the fall (Table 4). Additionally, the Yellow-breasted Chat was both highly frugivorous and a scrub-shrub breeder, and was also more numerous on Star Island.

Both vegetation structure and species composition can affect habitat suitability and use (Rice et al. 1984, Moore et al. 1995, Finch and Wang 2000). There were differences in plant species and

TABLE 3. Differences in vegetation physiognomy between Star Island and Appledore Island based on a Mann-Whitney *U*-test of means in each category; df = 1 for all tests. There were three plots (0.04 ha) on Star Island and five plots on Appledore Island. Data collected in 2000.

Category	Star Island		Appledore Island		*U*	*P*
	# stems	Mean/plot ± SD	# stems	Mean/plot ± SD		
Live trees						
Density	358	119.3 ± 95.30	986	197.2 ± 36.69	10.00	0.456
Height[a] (m)		3.1 ± 0.48		4.3 ± 0.44	15.00	0.025
Dbh[a] (cm)		4.4 ± 0.44		5.4 ± 0.71	14.00	0.053
Dead trees	13	4.3 ± 2.08	120	24.0 ± 14.05	15.00	0.025
Live shrubs						
Density	3,139	1,046.3 ± 80.71	1,341	268.2 ± 132.14	0.00	0.025
Height[a] (m)		1.3 ± 0.27		1.5 ± 0.23	11.00	0.297
Dead shrubs	919	306.3 ± 231.65	437	87.4 ± 65.89	2.00	0.101

[a] Mean per plot for each island was calculated from means of each individual plot on that island.

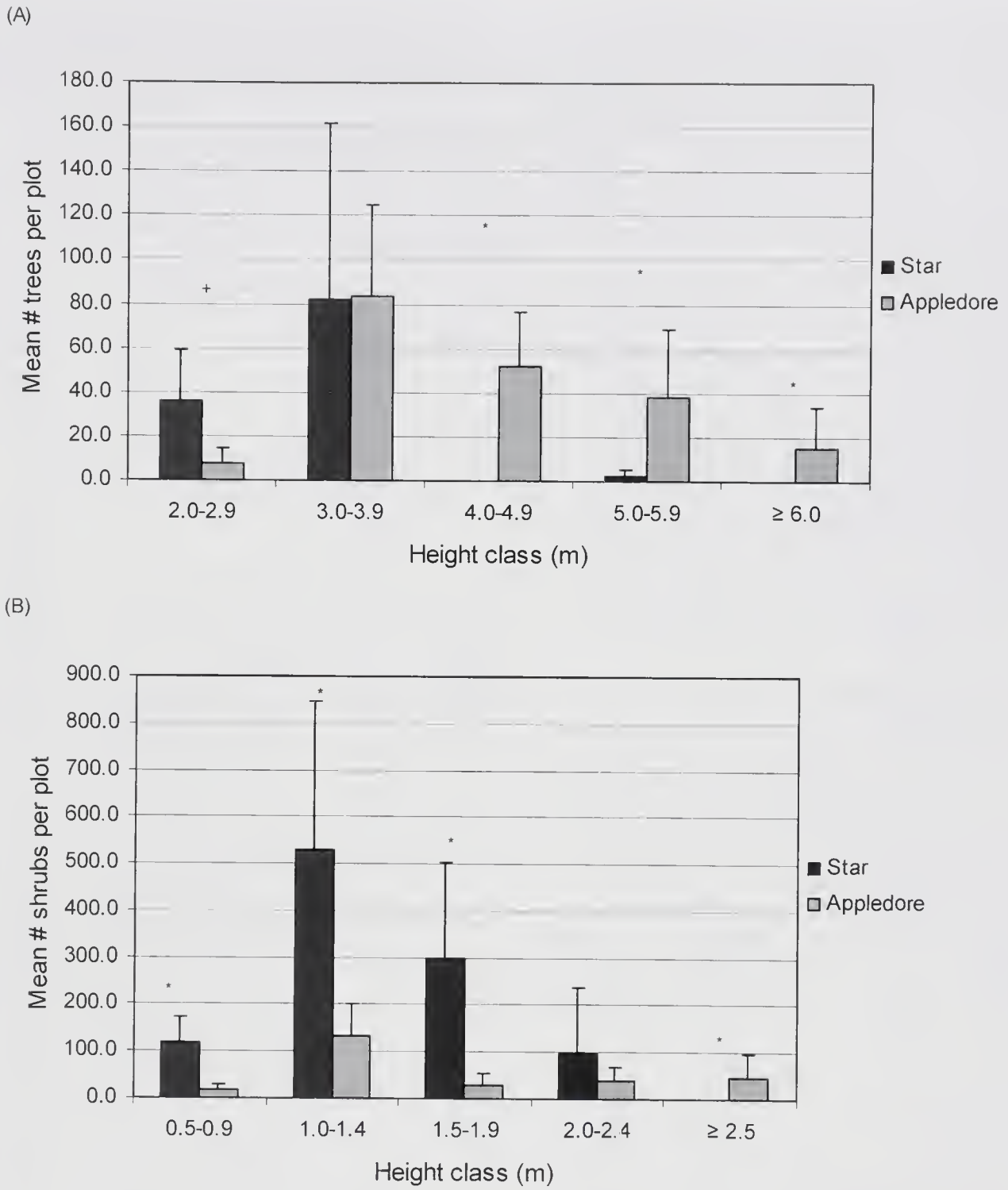

FIG. 1. Distribution of (A) trees and (B) shrubs by height class on Star Island, New Hampshire, and Appledore Island, Maine, in 2000. Bars are means ± SD; * = $P < 0.05$, and + = $0.05 < P < 0.10$.

vegetation structure between islands; the relative importance of these two factors is difficult to assess (Rice et al. 1984). Such was the case with Yellow-rumped Warbler, which feeds on bayberry during fall migration (Parrish 1997) and was more common on Star Island, the only island where bayberry occurred. However, the effect of habitat structure cannot be distinguished from the presence of bayberry (Kwit et al. 2004). The primary factor is likely structural differences for most species because migrants must adapt to a wide variety of plant species along their migration route, and species differences between islands were primarily based on breeding habitat structure.

Seasonal shifts in habitat have been observed at other sites (Winker et al. 1992, Weisbrod et al. 1993, Wang et al. 1998), but only Blue-headed Vireo in our study had a seasonal switch between islands. Thus, most species in this study were captured more frequently on the same island

TABLE 4. Ecological classifications for each avian species. SI = Star Island, AP = Appledore Island, – = no difference between islands, and blank = species not present in sufficient numbers to analyze. Area sensitivity without parentheses is from Robbins et al. (1989); in parentheses is from individual species accounts in The Birds of North America.

Species	More captures spr/fall	Area sensitivity (breeding)	Breeding habitat			Frugivory (fall)[c]
			General category[a]	Veg type[b]	Special characteristics	
Northern Flicker	/–	No	F-FE	M		
Eastern Wood-Pewee	–/–	No	F-FE	D-M		
Yellow-bellied Flycatcher	–/–	(No)	F-SF	C	Forests and bogs	Medium
Traill's Flycatcher	SI/SI	(No)	SS-FE	D		Med-hi
Least Flycatcher	–/–	(Yes?)	ES-F-FE	D-M		Medium
Eastern Phoebe	/–	(No)	FE	D-M		Med-hi
Blue-headed Vireo	AP/SI	No	F	C-M		Medium
Philadelphia Vireo	/–	(No)	F-FE-ES	D-C-M		Med-hi
Red-eyed Vireo	AP/AP	Yes	F-FE	D-M		Med-hi
Red-breasted Nuthatch	–/–	(No)	F	C-M	Mature forests	
Brown Creeper	/AP	No	F	C-D-M	Mature forests	Low
Golden-crowned Kinglet	/–	(No)	F	C		Low
Ruby-crowned Kinglet	SI/SI	(No)	F	C-M		Low
Vcery	–/AP	Yes	F	D	Dense understory	Med-hi
Swainson's Thrush	AP/–	(Yes?)	F-FE-ES	C-M		Med-hi
Cedar Waxwing	SI/SI	No	FE	D	Fruit/berry producers	High
Nashville Warbler	–/–	(No)	ES-F-FE	C-D-M		Medium
Northern Parula	–/–	Yes	F-FE	C-D-M	Mature forests	Medium
Chestnut-sided Warbler	–/–	No	SS-ES-FE	D	Densc low growth	
Magnolia Warbler	SI/SI	No	F-ES	C-M	Densc understory	Med-hi
Black-throated Blue Warbler	AP/AP	Yes	F	D-M	Densc sapling/shrub understory	Medium
Yellow-rumped Warbler	SI/SI	(No)	F	C-M		Med-hi
Black-throated Green Warbler	–/–	No	F	C-M	Mature forests	Medium
Blackburnian Warbler	–/	(No)	F	C-M	Mature forests	
Blackpoll Warbler	–/–	(No)	F-SF	C	Low northern spruce	Medium
Black-and-white Warbler	AP/AP	Yes	F	D-M	Forests with saplings	Low
American Redstart	–/AP	No (Yes?)	ES-F-FE	D	Thick sapling understory	Low
Ovenbird	AP/AP	Yes	F	D-M	Mature forests	Medium
Northern Waterthrush	AP/AP	Yes	F-FE	D	Wetland/pond edges	Med-hi
Mourning Warbler	AP/–	(No)	SS-ES	D-M	Dense saplings/shrubs	Med-hi
Wilson's Warbler	SI/SI	(No)	SS-SF	D		Low
Canada Warbler	AP/–	Yes	F	D-M	Dense understory	Low
Yellow-breasted Chat	/SI	No	SS-FE	D	No overstory	High
Savannah Sparrow	SI/	(No)	O	G		
Lincoln's Sparrow	–/SI	(No)	SS-FE-SF	D-M		Med-hi
Swamp Sparrow	SI/SI	(No)	SS	D-G	Wetlands	Medium
White-throated Sparrow	–/SI	(No)	FE-ES-SF	D-C-M	Brushy understory	Med-hi
Rose-breasted Grosbeak	–/	Yes	FE-F	D		High
Baltimore Oriole	–/–	No	FE	D		
Purple Finch	SI/SI	(No)	F-FE	C-M		High

[a] Habitat categories: ES = early successional, F = forest, FE = forest edge, SF = short forests at high elevation and in bogs, SS = scrub/shrub, and O = open areas, grasslands, emergent wetlands.

[b] Vegetation type (veg type), C = coniferous, D = deciduous, G = grassland/sedge/reed, and M = mixed coniferous-deciduous.

[c] Frugivory based on mean percentage of fruit in fecal samples (Parrish 1997): low 0–29, medium 30–59, medium-high (med-hi) 60–89, high 90–100%, and blank = not in analysis.

during both spring and fall. The consistency of habitat selection by a wide range of migrant species between spring and fall supports the hypothesis that habitat selection in passerines is endogenous (Bairlein 1983, Morton 1990, Winker 1995). Migrant distribution might be expected to change between spring and fall, after the large proportion of young migrants have had more exposure to a variety of habitats on both their southward and return migrations, if habitat

selection was learned. Additionally, the correlation of stopover habitat with breeding habitat indicates innate preferences as suggested by Moore et al. (1995).

The apparent association with breeding habitat by migrants during stopover is consistent with Petit's (2000) analysis of habitat selection in five studies. Smaller physiognomic and plant species differences between islands were associated with differences in species distribution between islands. Our study suggests stopover habitat use was related to habitat structure, plant species, diet (extent of frugivory), and habitat area, but the predominant factor(s) may differ among species.

Habitat differences between these two islands were smaller in structure and species type than described in other stopover habitat studies (e.g., Bairlein 1983, Moore et al. 1990, Rodewald and Brittingham 2004); but differences between islands were associated with differences in bird species distribution. Nocturnal migrants typically land when it is still dark and are unlikely to make stopover decisions based on these small habitat differences. Migrants may conduct habitat exploration flights during the day (Moore and Simons 1992, Wiedner et al. 1992), but few birds banded on one island were recaptured on the other island (Suomala 2005) indicating little movement after initial landing. We suggest several mechanisms to explain the detection of small habitat differences: (1) migrants may be landing at the Isles of Shoals later in the morning than migrants at other locations and are able to see detailed habitat features; (2) migrants may be able to see certain features in the dark; and/or (3) there is a non-visual component of stopover habitat selection, similar to the vocal social cuing that Betts et al. (2008) reported was more important than vegetation structure in habitat choice for breeding site selection.

CONSERVATION IMPLICATIONS

Priority stopover habitat for the bird community may be difficult to define due to differing habitat preferences of individual species (Hutto 2000, this study). Protection of stopover sites with a wide variety of habitats, both forest and scrub-shrub, is important to meet the needs of migrant passerines (Weisbrod et al. 1993, Rodewald and Brittingham 2004, this study).

The species-specific differences in habitat use in this study suggest migrants are not using the Isles of Shoals as simply emergency stops, landing at random out of desperation. Scrub-shrub habitat is naturally occurring on the coastal plain and a good source of berry-producing shrubs, which may be one of the best areas for migrants to deposit fat (Parrish 1997). Other studies have demonstrated the importance of edge and shrubland habitats with fruit to fall migrants (Parrish 1997; Suthers et al. 2000; Rodewald and Brittingham 2002, 2004), but the management of scrub-shrub habitat for migrants may be overlooked as an important priority.

Land use changes along the coast are occurring rapidly with resulting deterioration of stopover habitat (Mabey and Watts 2000). Coastal development creates a landscape that is often inhospitable to migrating birds. Conservation efforts for migrant songbirds should encompass the remaining small patches of natural habitat that may be critical to migrant survival (Blake 1986). Education and local land use policies may be effective tools for maintaining small habitat patches on private lands (Mabey and Watts 2000).

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CONCENTRATED MIGRATORY MORNING FLIGHT AT LAKE PONTCHARTRAIN, LOUISIANA, USA

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ABSTRACT.—I describe large volume morning flights of migrant songbirds in autumn along the south shore of Lake Pontchartrain, Louisiana, USA. These flights have at times exceeded 10,000 birds/hr since their discovery in 2002, ranking the site among the continent's highest volume regular migratory songbird concentration locations. Migrants move in "reverse" direction northeastward up a peninsula in Lake Pontchartrain, and fly across a 9-km water gap to reach the north shore, usually struggling into a headwind. Flights are dominated by Yellow and Yellow-rumped warblers (*Dendroica petechia* and *D. coronata*), Eastern Kingbird (*Tyrannus tyrannus*), Indigo Bunting (*Passerina cyanea*), Cedar Waxwing (*Bombycilla cedrorum*), and American Robin (*Turdus migratorius*) during their respective migratory peaks. These species have exceeded 800 birds/hr, and 70 other small landbird species have been recorded. Flights of >100 birds/hr were more frequent after nights with more hours of northerly winds. *Received 24 August 2009. Accepted 30 April 2010.*

The Nearctic-neotropical migratory system involves the movement of billions of birds southward within the Western Hemisphere, some staying within temperate latitudes and others traveling to the Neotropics. The major barrier to the large contingent of migrants headed from eastern North America to tropical America is the Gulf of Mexico, which many species cross in a single extended flight. The dynamics of this trans-Gulf movement have been most extensively studied in spring. Northbound migrants normally arrive on the central Gulf Coast during daylight, often after having flown ≥6 hrs longer than in a normal overland nocturnal flight. Arriving trans-Gulf migrants normally over-fly coastal regions and disperse into habitats >100 km inland, causing near-coastal areas to be labeled the "coastal hiatus" (Lowery 1945). Their reasons for passing far inland before alighting are unknown, but the paucity of forest cover in the wetland landscape adjacent to the coast is a likely factor. Fall movements are even more poorly understood. Able (1972) noted that weather conducive to forward migration is more limited in fall than spring when prevailing southeasterly winds impede crossing the Gulf except when broken temporarily by the passage of cold fronts with their accompanying northerly tailwinds.

The objectives of this paper are to: (1) report the existence of an unusual migratory movement phenomenon at Lake Pontchartrain, Louisiana, and (2) discuss the insights it provides into the dynamics of autumnal migration on the Gulf Coast. The volume of bird movement discovered to occur here ranks this newly discovered site as one of the major migratory songbird concentration locations in the Western Hemisphere.

METHODS

Study Site.—Lake Pontchartrain is ~100 km north of the Gulf of Mexico, from which it is separated by urban New Orleans and expansive wetlands (Fig. 1). The city extends 10–20 km southward from the central portion of the lake, while wetlands border the lake's southwestern and southeastern flanks, the latter on the Bayou Sauvage National Wildlife Refuge. The landscape outside the southern hurricane-protection levee of the city changes abruptly to bottomland hardwood and swamp forests, which transition southward through shrub-dominated wetlands into open fresh and brackish marshes, and finally to salt marsh that is flanked in some places by barrier islands and headlands. Several large semi-tidal lakes and inlets penetrate nearly as far northward as the city. The corridor of the Mississippi River winds through the city before heading southeast to the Gulf, its ≤3 km fringe of flanking field and woodlots forming the largest contiguous area of dry land south of the city.

Lake Pontchartrain is roughly oval in shape, 39 km north-south and 65 km east-west at its widest, but is pinched by the extension of a peninsula northward near its eastern end that reduces the overwater distance to 9 km. This peninsula ends at two adjacent points of land, South Point and Pointe aux Herbes (Fig. 1C, D), from which railroad and highway bridges depart for the north shore. Migratory songbird movements are greatest on this peninsula, especially progressing northward up its western flank and departing from either of these two points to cross the lake.

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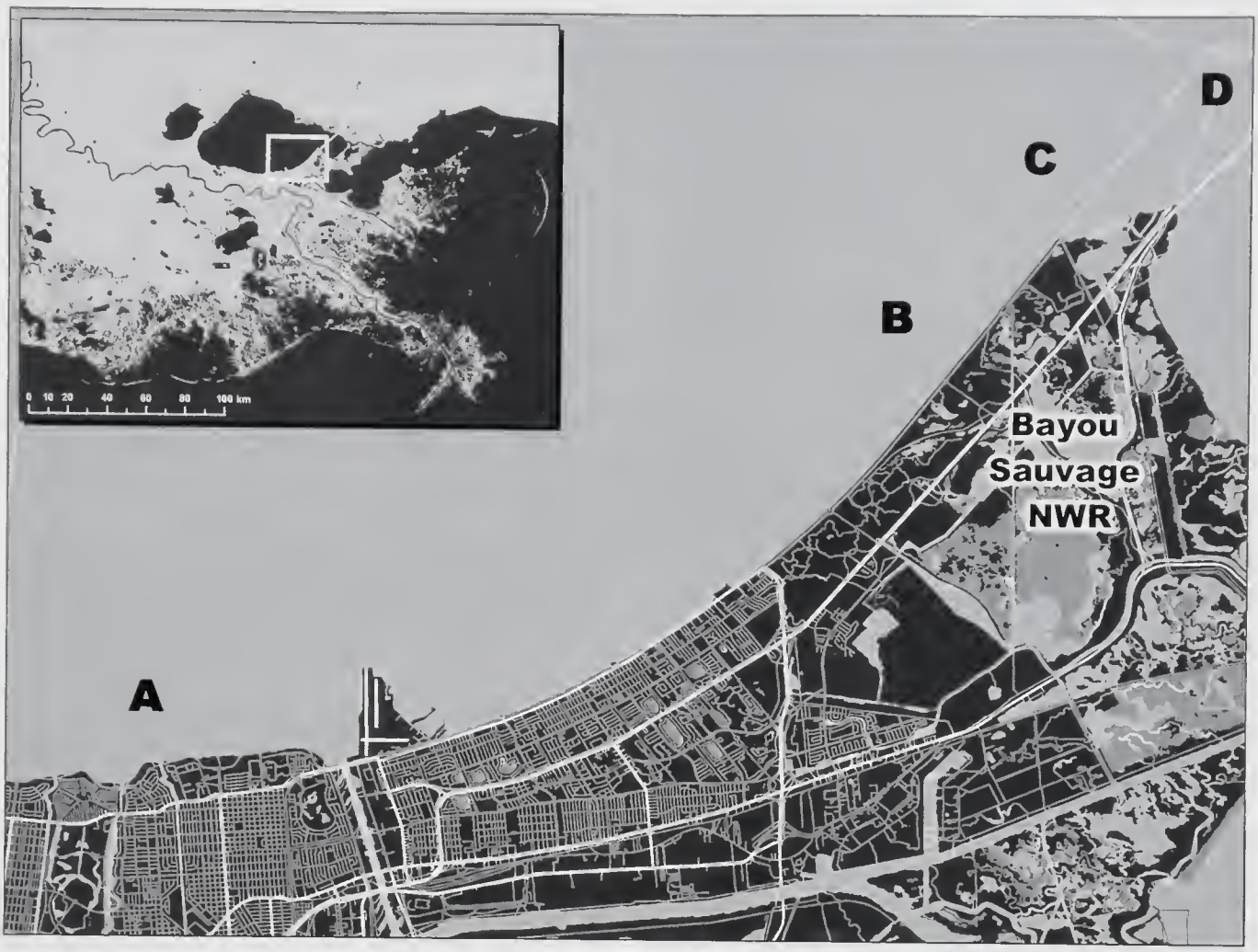

FIG. 1. Study area showing locations where major morning movements have been recorded: (A) University of New Orleans; (B) Bayou Sauvage National Wildlife Refuge bicycle path; (C) South Point; (D) Pointe aux Herbes. Map by Steve Stevens and John Adams.

Northward curvature of the Gulf shoreline wraps open wetland and coastal lakes north to the east of Lake Pontchartrain, and essentially no forest cover lies east or southeast of its eastern end. Pine (*Pinus* spp.) forest is absent south of Lake Pontchartrain, but is common on its north shore.

Field Procedures.—Preliminary scouting of morning flight was conducted by visiting several coastlines and land-marsh interfaces near Lake Pontchartrain in fall 2002. Systematic collection of data began in fall 2003, when volunteer observers were stationed at Pointe aux Herbes (Fig. 1D) to document movement of birds across the water gap and find correlations with weather patterns recorded at Lakefront Airport (Fig. 1 between sites A and B). Additional visits were made to sites C and D through 2009, mostly on days with northerly winds with the frequency of visitation declining after Hurricane Katrina in 2005. Observers counted birds passing their observation point in 15-min intervals starting near dawn, and typically lasting 1–3 hrs.

I used surface wind data because of their hourly resolution, despite their differing at times from winds aloft at the altitude of nocturnal migration. The number of nocturnal hours of northerly (between WNW and ENE) winds was tabulated preceding each flight count because, in the case of the cold front passages that usually preceded the diurnal movements noted, the number of hours of post-frontal conditions before daybreak may affect the opportunity for nocturnal migrants to be wind-drifted south of the lake. Bird counts conducted over ≥30 min were used to calculate hourly passage rates.

RESULTS

The presence of significant diurnal song bird movements along the Lake Pontchartrain peninsula was not discovered until 22 November 2002, although local observers had infrequently visited this peninsula in previous years and occasionally noted migratory birds moving in anomalous directions. A continuous heavy movement of

TABLE 1. Peak rates of hourly and daily passage for selected species at Lake Pontchartrain, Louisiana, USA.

Species	Peak hourly passage (date)	Peak daily passage[a] (date)
Eastern Kingbird	25,000 (5 Sep 2003)	35,000 (5 Sep 2003)
American Robin	12,000 (28 Nov 2004)	20,000 (28 Nov 2004)
Cedar Waxwing	3,500 (22 Nov 2002)	7,000 (22 Nov 2002)
Yellow Warbler	800[b] (31 Aug 2004)	1,200 (23 Aug 2009)
Yellow-rumped Warbler	4,500 (22 Nov 2002)	12,500 (23 Nov 2002)
Indigo Bunting	880 (15 Oct 2002)	1,000 (15 Oct 2002)

[a] All counts were obtained during ≤3 hrs of counting.
[b] Extrapolated from 41 min observation.

songbirds northeastward along the western flank of the peninsula (Fig. 1B) was witnessed on the morning of 22 November 2002 following a cold front passage. Frequent timed counts over 2 hrs produced an estimated total of 25,000 birds dominated by American Robins (*Turdus migratorius*), Cedar Waxwings (*Bombycilla cedrorum*), and Yellow-rumped Warblers (*Dendroica coronata*). These birds were flying low into the NNE wind, using a narrow tree row that separated the lake levee from the landward marshes as a windbreak. The next morning another 18,500 birds were estimated to pass up the shore in 3 hrs at this site, dominated by the same species. Over the next few weeks, as the fall migration dwindled, similar but smaller bird movements were tracked up the peninsula and found to be crossing the lake at South Point and Pointe aux Herbes (Fig. 1C, D). The lakeshore along this western flank of the peninsula is not readily accessible, being behind gated roads within the Bayou Sauvage National Wildlife Refuge.

A few morning songbird flights detected earlier in the same fall at a site 0.5 km south of the lakefront and near the western base of the peninsula seemed in retrospect to have represented similar patterns of movement, but for neotropical migrant species (Fig. 1A). On 5 September 2002, ~1,400 Eastern Kingbirds (*Tyrannus tyrannus*) were counted in 1 hr flying ENE parallel to the lakefront, and on 15 October, ~1,350 small songbirds, predominantly Indigo Buntings (*Passerina cyanea*), had been seen passing northward toward the nearby lakeshore in 68 min; their behavior upon reaching the shore was not identified.

Flights exceeding 100 birds/hr were observed on 37 days each fall during 2002–2004, and occurred as early as 8 August and as late as 28 January. Subsequently, flights have been detected as early as 13 July 2008 (proceeding up the Mississippi River south of the lake). The largest flights have occurred during peak passages of Yellow Warblers (*Dendroica petechia*) and Eastern Kingbirds in August–September, Indigo Buntings in October, and American Robins, Cedar Waxwings, and Yellow-rumped Warblers in November. Counts during northeast winds have repeatedly exceeded 1,000 birds/hr, and six individual species have peaks of >500/hr with robin and kingbird counts surpassing 10,000/hr (Table 1). Species identification of many of the less frequent species was difficult until 2004, when more visits were made to site C, which has the best viewing conditions. Seventy-two species of small migratory land birds, mostly nocturnal migrants, were identified as they crossed or attempted to cross the lake at sites C and D from 2003 to 2009.

All significant movements recorded at the lakefront have been northeastward, except for seven oriented at a bearing west of north in departing across the water from the western point (South Point, site C). These directions result in a longer overwater crossing and have only occurred when morning winds were from west of north.

Wind directions were analyzed for flights from 2002 through 2004, the most consistent period of field observation (Fig. 2). Flights peaking at ≥100 birds/hr occurred with differing frequency when different numbers of hours of northerly winds had occurred the night before ($\chi^2 = 23.0$, $n = 108$, $P = 0.0017$). They occurred on a majority of mornings following ≥9 hrs of northerly winds, but less than a tenth of those with ≤2 hrs. Northerly winds are unusual on the Gulf Coast except after frontal passages, which were infrequent in August but frequent each November during the study. Thus, the northerly winds conducive to mass movements at the lake are more common during late fall periods dominated by temperate zone migrants. Another source of

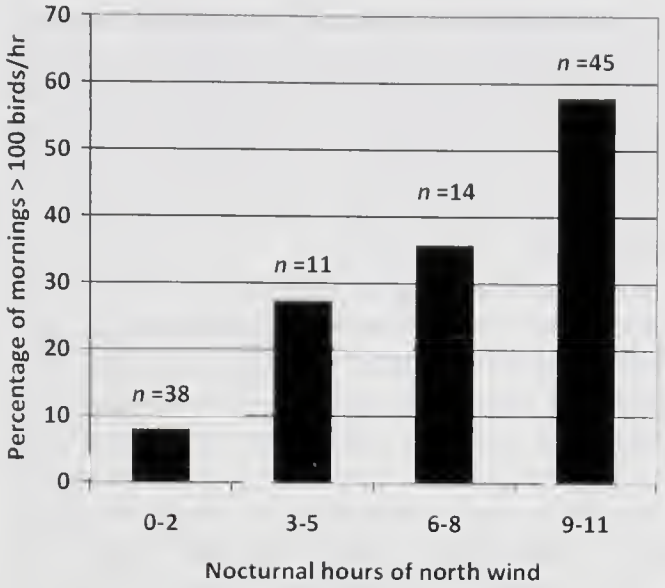

FIG. 2. Percentage of days with morning movements >100 birds/hr that followed nights with different hourly frequencies of northerly winds.

northeast winds in early fall has been the occasional tropical cyclone that has entered the eastern Gulf of Mexico; Tropical Storm Henry produced northeast winds during the massive kingbird movement on 5 September 2003 (Table 1), while 550 km to the ESE near the Florida coast.

DISCUSSION

Why are there regular northward movements of migrant birds across Lake Pontchartrain on mornings after fall cold fronts? There are three potential explanations. (1) The movements represent forward migration of birds attempting to head eastward, but detouring northward to avoid the open Gulf and marshes ahead to the east. (2) The movements represent migrants not attempting forward progress, but searching locally for suitable stopover habitat in which to rest or feed. (3) The birds are making a corrective movement to compensate for wind drift or navigation errors.

The first hypothesis of detoured forward migration is appealingly simple, but contradicts the basic widespread recognition that circum-Gulf migration in Louisiana is westbound (e.g., Lowery 1974). This has been established by radar (Able 1972), visual studies of morning flight (Duncan and Weber 1985), and cage orientation studies (Sandberg and Moore 1996). Other weaknesses include: (1) birds on some dates move primarily NW, (2) it seems unlikely that large numbers of birds would migrate forward into headwinds (yet most heavy flights are during NE winds), and (3) birds seldom approach the overwater crossing up the east side of the peninsula as would be expected if birds were detouring from the south as proposed.

The second hypothesis, that birds are seeking foraging and resting habitat is consistent with the patchiness of forest and scrub habitats south of the lake. The overwhelming dominance of northbound birds at the peninsula could be a consequence of shoreline configuration—only northbound birds are able to approach the peninsula overland, and the lakeshore concentrates birds approaching from that direction. At least one species, Tree Swallow (*Tachycineta bicolor*), appears to commute across the lake in its daily search for food. This winter resident regularly forms nocturnal roosts in late fall in sugar cane (*Saccharum officinarum*) fields 80 km to the southwest that may include over a million birds (Seymour 2009). I attributed large Tree Swallow flights (e.g., 18,000 in 1.5 hrs on 6 November 2004) to roost dispersal and omitted them from this analysis, but it is difficult to imagine most other songbirds crossing the lake as commuters. The capacity of swallows for strong flight as they depart across the lake contrasts with the greater struggle of many other songbirds. Some species have so much difficulty that they appear to make repeated failed departures in short order; for instance 100 departures by Golden-crowned and Ruby-crowned kinglets (*Regulus satrapa* and *R. calendula*) in 7.5 min on 2 November 2005 appeared to involve many repeat attempts to cross the lake. It is difficult to imagine that searching behavior would have such a strong northeastward impulse (or into-wind impulse) that birds would be willing to cross 9 km of water into a headwind, expending energy and potentially exposing themselves to accipiters and falcons that are common on the peninsula in autumn. This would also fail to explain why other resident songbirds do not engage in such flights (only Rock Pigeons [*Columba livia*] do so regularly, and usually southbound), and why flights of Yellow-rumped Warblers and American Robins dwindle precipitously in mid-winter despite remaining numerous in the region. Searching for food may contribute to cross-lake movements by some species, but does not appear to be a sufficient explanation for most.

The third hypothesis, corrective movement, is favored in part because it has been cited as the explanation for coastal retreat movements along the Atlantic shoreline of northeastern North

America including at Cape May, New Jersey (Baird and Nisbet 1960) and in Sweden at Falsterbo, a site where diurnal reverse-directional movements are also massive in fall (Alerstam and Ulfstrand 1975, Alerstam 1978, Akesson et al. 1996). Swainson's Thrushes (*Catharus ustulatus*) on the northern Gulf Coast have also been observed to orient inland in flight cages in the early morning when they are in lean body condition in fall, as did lean Red-eyed Vireos (*Vireo olivaceus*) released at night (Sandberg and Moore 1996, Sandberg et al. 2002). That migrants would exhibit a directional response to remove themselves from the coastal 100 ± km of Louisiana is also consistent with the knowledge they appear to find these areas unsuitable during spring, normally flying over them when arriving from a spring Gulf crossing (Lowery 1945, Gauthreaux 1971). Fall migrants intending to winter in the region could also backtrack if they find the coastal wetlands unsuitable wintering habitat. The northward direction of both neotropical and temperate migrants could be either a reflection of attempting to backtrack to an earlier position on the migratory route before habitat became inhospitable, or of attempting to compensate for wind drift by retreating into the wind, which is generally northerly after nights of heavy migration in fall. Other authors have reported changes in diurnal flight orientation to compensate for nocturnal wind drift (Baird and Nisbet 1960, Able 1977, Gauthreaux 1978, Moore 1990), and apparent reversal of migratory orientation over inhospitable areas (DeSante 1973, Thorup and Rabøl 2007). Migrants might retreat because wind drift has carried them farther south than intended on that date in their migration in addition to avoiding inhospitable habitat. Some large flights at South Point have involved species that did not arrive in numbers elsewhere in coastal Louisiana until weeks later (e.g., 7,000 Cedar Waxwings on 22 November 2002).

The occurrence of large movements of American Robins and Cedar Waxwings along the Gulf Coast is interesting because the Gulf Coast forms the southern edge of their wintering ranges at this longitude. The large flights of Yellow-rumped Warblers, occurring mainly in late November, may also represent temperate winterers rather than trans-Gulf migrants, as the bulk of other trans-Gulf migrant species have departed the northern Gulf Coast by 1 November (Lowery 1974). The other major concentration sites of migrants in North America usually involve birds well north of their southern range limits, at latitudes traversed by a large portion of the population during their migration. Large flights near these species' southern range limits are surprising, because relatively small proportions of their populations migrate this far south.

The evidence suggests the movements observed along Lake Pontchartrain are predominantly birds retreating from coastal wetlands. If correct, this adds an important detail to the dynamics of migration near the Gulf Coast. It indicates the "coastal hiatus" phenomenon for neotropical migrants long documented for spring migration has a counterpart in fall. In the case of temperate zone migration, it indicates that overshoot of wintering areas by a short distance (~100 km) along the Gulf Coast is a common phenomenon. In either case, the species involved must incur a stressful upwind flight to *terra firma* that may take several hours and deplete energy reserves. It also implies, in the case of neotropical migrants, that habitats lying just north of the coastal wetlands might be especially important as stopover sites forming the last stops before the demanding trans-Gulf flight.

The numbers of birds involved in the Lake Pontchartrain flights make it one of only a handful of places in North America where diurnal movements of migrant song birds (excluding swallows) are documented to regularly exceed 1,000 birds/hr. These include sites along the Atlantic shoreline from Long Island Sound to Delaware Bay (e.g., Lighthouse Point, Connecticut and Cape May, New Jersey), on the shorelines of Lake Erie and Lake Ontario (e.g., Holiday Beach, Ontario, and Braddock Bay, New York), at Tadoussac on the north shore of the St. Lawrence River in Quebec, and along the Gulf of Mexico shoreline near Veracruz, Mexico. It is unusual in its inclusion of a 9 km elective overwater flight (as opposed to return to land from the ocean), although southbound Blue-gray Gnatcatchers (*Polioptila caerulea*) regularly make an overwater crossing at Smith Point on the Texas coast (John Arvin, pers. comm.). The predominant species are those known to be at least partially diurnally migratory, as is the case elsewhere. Most have large regular diurnal movements at one or more of these other localities, except apparently the Indigo Bunting. Large flights are characteristically accompanied by other species, including a wide variety of nocturnal migrants. However, many

understory species apparently do not cross the lake as no attempts have been observed by catbirds, thrashers, *Catharus* and *Hylocichla* thrushes, and wrens; the only sparrows have been those of the most open habitats (e.g., Savannah Sparrow [*Passerculus sandwichensis*]).

If flights represent northward corrective movements, they might be less common along the eastern half of the northern Gulf Coast, which lacks the wide expanse of coastal wetlands that lie south of Lake Pontchartrain. Broad wetlands border the coast for 500+ km west from the mouth of the Mississippi River throughout Louisiana and the upper coast of Texas, and these would seem good candidates for reverse flights. However, without a funneling geographic feature, these flights might not be concentrated as they are at Lake Pontchartrain. The 40-km shoreline of Lake Pontchartrain apparently turns an otherwise diffuse northward movement into a spectacle. If one assumes that birds arrive at South Point or Pointe aux Herbes after accumulating along the lakeshore as they arrive from the south and detour eastward, then arrival of only five northbound birds/hr at each 0.1 km of lakefront (estimating the detection range of an urban observer on the ground) would accumulate into a flight of 2,000 birds/hr at the peninsula. These concentrating factors are probably lacking elsewhere in the coastal wetlands, but study of movement patterns of migrants throughout the area would be worthwhile, and may provide insights regarding which areas are most critical to their preparations to cross the Gulf of Mexico.

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NIGHT MIGRANT FATALITIES AND OBSTRUCTION LIGHTING AT WIND TURBINES IN NORTH AMERICA

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ABSTRACT.—Avian collision fatality data from studies conducted at 30 wind farms across North America were examined to estimate how many night migrants collide with turbines and towers, and how aviation obstruction lighting relates to collision fatalities. Fatality rates, adjusted for scavenging and searcher efficiency, of night migrants at turbines 54 to 125 m in height ranged from <1 bird/turbine/year to ~7 birds/turbine/year with higher rates recorded in eastern North America and lowest rates in the west. Multi-bird fatality events (defined as >3 birds killed in 1 night at 1 turbine) were rare, recorded at <0.02% ($n = 4$) of ~25,000 turbine searches. Lighting and weather conditions may have been causative factors in the four documented multi-bird fatality events, but flashing red lights (L-864, recommended by the Federal Aviation Administration [FAA]) were not involved, which is the most common obstruction lighting used at wind farms. A Wilcoxon signed-rank analysis of unadjusted fatality rates revealed no significant differences between fatality rates at turbines with FAA lights as opposed to turbines without lighting at the same wind farm. *Received 30 May 2006. Accepted 29 June 2010.*

Songbirds often collide with communication towers, lighthouses, skyscrapers, and other structures during nocturnal migration with fatalities, at times, numbering in the hundreds or even thousands of birds in a single night (Banks 1979, Avery et al. 1980, Trapp 1998, Kerlinger 2000). Research suggests lighting has a primary role in attracting or disorienting night-migrating songbirds at those structures, especially during overcast, foggy, or rainy conditions (Cochran and Graber 1958, Caldwell and Wallace 1966, Avery et al. 1976). Many studies, attempting to assess how lights influence bird behavior, have focused on communication towers. Larkin and Frase (1988) used tracking radar to show that, during fog and low cloud ceiling, night migrants circled a >305-m tall communication tower with Federal Aviation Administration (FAA)-approved obstruction lighting, but departed the tower when lights were extinguished. Gauthreaux and Belser (2006) used marine surveillance radar and infrared scopes to compare night migrant activity at two tall (>305 m), lighted communication towers with guy wires and at a separate control plot. One of the towers had flashing and steady-burning red lights, the other had only flashing white strobe lights. They found that birds flew in straight flight paths over the control plot but, at the lit towers, flight paths were curvilinear and birds concentrated near the towers. More birds concentrated at the tower with flashing and steady-burning red lights than at the tower with flashing white strobe lights. This led Gauthreaux and Belser (2006) to suggest that research was needed to improve understanding of the attraction of different obstruction lighting systems to night-migrating songbirds.

A recent study in Michigan by Gehring et al. (2009) of 24 communication towers with different heights, support systems, and lighting found that towers lit at night with only flashing red or white lights had significantly fewer avian fatalities than towers lit with a combination of steady-burning and flashing lights. These results suggest avian fatalities can be reduced, perhaps by 50–71%, at communication towers supported by guy wires by replacing steady-burning lights with flashing lights.

Avian collision fatalities are well documented at wind turbines (turbine rotor or tower), but the estimated total number of birds killed annually is small relative to communication towers and other structures (Erickson et al. 2005, National Research Council 2007). Wind turbines >60 m in height are often equipped with FAA-approved obstruction lighting, but not all turbines need to be lit, as long as gaps between lighted structures do not exceed 0.8 km (FAA 2000). Thus ~25–33% of turbines at most wind farms should have obstruction lighting on the nacelle (where the

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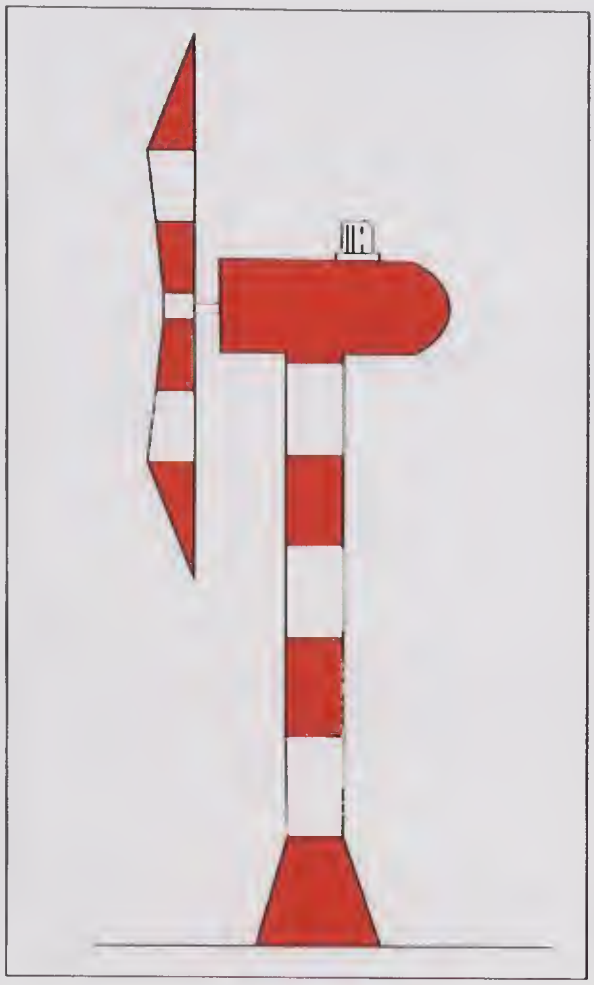

FIG. 1. Wind turbine showing location of Federal Aviation Administration obstruction lights on the nacelle.

blades are attached to the rotor hub; Fig. 1) adjacent to where the rotors are attached. The FAA (2000) recommends flashing red lights be placed on the turbine nacelle but flashing white and steady-burning red lights have also been used on a limited number of turbines. The flashing red lights are model L-864, a red strobe, LED (light-emitting diode), or pulsating incandescent light that flashes 20–40 times/min with an intensity of 2,000 candela. Steady-burning red lights are classified as model L-810, an incandescent red lighting that has a minimum intensity of 32.5 candela. L-810 lights are red and occasionally are modified to flash. Flashing white lights are classified as model L-865 and are a white strobe typically set at 40–60 flashes/min with an intensity of up to 2,000 candela. These same types of obstruction lights are used on communication towers (FAA 2000, Gehring et al. 2009).

Concerns about avian mortality have prompted fatality studies at wind farms across the United States and Canada. Most studies are available as reports to meet permit requirements and are often reviewed by state and federal wildlife agencies. This paper reviews existing information on night migrant mortality at wind farms derived from 31 studies at 30 wind farms. Our objectives were to: (1) examine the incidence of multi-bird fatality events at individual wind turbines and their relationship with lighting, and (2) examine whether disproportionately greater numbers of fatalities occur at turbines equipped with FAA-approved lights as opposed to turbines without approved lights.

METHODS

Data were extracted from post-construction, avian fatality studies conducted at 30 wind farms across the United States and Canada (Table 1). Studies prior to 1995 were not included because turbines lacked obstruction lighting and were <50 m in height (to maximum blade tip height). Excluded studies in this category were conducted at Altamont Pass Wind Resource Area, San Gorgonio Pass, and Tehachapi Mountains, all in California. The results of studies at several small wind farms conducted after 1995 were also not included because lighting or search methodologies could not be verified. Other wind farms in the United States and Canada were not included because they have not been studied or, if they have been studied, reports were not available.

Data extracted included geographic region; turbine nameplate production in megawatts (MW); turbine height (to the maximum blade tip height); total number of turbines in the wind farm and the subset of turbines studied; lighting type, including the total number of turbines with lighting and the number of lit turbines studied; study duration and search interval during migration seasons; unadjusted number of nocturnal migrant carcasses found; and estimated fatality rate (birds/turbine/year). Carcasses were assigned as night-migrating songbirds or similar species (i.e., cuckoos, etc.) based on migration tendency (nocturnal vs. diurnal) and date recorded.

Methodologies for studying collision mortality at wind farms varied, but basically followed accepted practices (e.g., Anderson et al. 1999). Carcass searches were usually conducted every week to 1 month in the western United States, whereas they were usually conducted every 1–2 days to 1 month in the eastern United States and Canada. Some studies used different search intervals at different subsets of turbines. Searchers

TABLE 1. Estimated avian migrant mortality per year (spring and fall) from 31 studies at 30 wind farms (Buffalo Mountain studies were done at each of the 2 types of turbines on site).

Location	Turbine type (total/study)	Turbine height (m)	Lighting type (total/study)	Study duration	Search interval during migration	Observed nocturnal migrant fatalities/yr	Estimated fatalities/turbine/yr	Reference
Western U.S.								
High Winds, CA	1.8 MW (90/90)	100	Flashing red (26/26)	2 years	14 days	15	<1/turbine/yr	Kerlinger et al. 2006
Ponnequin, CO	0.66–0.75 MW (44/44)	79	Flashing red (21/21)	5 years	7 days–1 month	5	<1/turbine/yr	Kerlinger and Curry 2000, unpubl. data
Judith Gap, MT	1.5 MW (90/20)	119	Flashing red (30/7)	7 months	1 month	6	~2–3/turbine/yr	TRC Env. Corp. 2008
Klondike, OR	1.5 MW (16/16)	100	Flashing red (9/9)	1 year	1 month	4	<1/turbine/yr	Johnson et al. 2003
Vansycle, OR	0.66 MW (38/38)	74	Flashing red (11/11)	1 year	14–28 days	5	<1/turbine/yr	Erickson et al. 2000
Stateline, OR/WA	0.66 MW (454/124–153)	72	Flashing red (~140/~45)	2.5 years	0.5 months	20	<1/turbine/yr	Erickson et al. 2004
Nine Canyon, WA	1.3 MW (37/37)	91	Flashing red (15/15)	1 year	2 weeks	7	<1/turbine/yr	Erickson et al. 2003
Foote Creek Rim, WY	0.60 MW (69/69)	61	None	3.5 years	14–28 days	12	<1/turbine/yr	Young et al. 2003
Central U.S.								
Top of Iowa, IA	0.90 MW (89/26)	98	Steady red, flashing red, and flashing white (89/26)	2 years	2 days	2.5	<1/turbine/yr	Jain 2005, Koford et al. 2005
Crescent Ridge, IL	1.5 MW (33/33)	120	Steady red and flashing red (10/10)	7 months	5 days	5	<1/turbine/yr	Kerlinger et al. 2007
Buffalo Ridge, MN	0.36–0.75 MW (354/111)	54–76	Steady red and flashing red (75/~25)	4 years	2 weeks	10	~3/turbine/yr	Johnson et al. 2000, 2002
Ainsworth, NE	1.5 MW (36/36)	110	Flashing red (24/24)	7 months	2 weeks	18	~2.5/turbine/yr	Derby et al. 2007
Blue Canyon II, OK	1.8 MW (84/50)	~125	Flashing red (38/23)	7.5 months	1 week	2	<1/turbine/yr	Schnell et al. 2007
Buffalo Gap I, TX	2.0 MW (67/21)	~120	Probably flashing red (21/~6?)	10 months	~1 month	6	<1/turbine/yr	Tierney 2007
Kewaunee, WI	0.66 MW (31/31)	89	Flashing red (22/22)	2 years	0.5 weeks	5	<1/turbine/yr	Howe et al. 2002
Eastern U.S.								
Mars Hill, ME	1.5 MW (28/28)	119	Flashing Red (10/10)	2 years	1–7 days	18	~2–3/turbine/yr	Stantec 2008, 2009
Atlantic County, NJ	1.5 MW (5/5)	116	Flashing red (5/5)	7 months	~2 days	9	Not estimated	NJ Audubon 2008
Bliss, NY	1.5 MW (67/23)	119	Flashing red (21/7)	8 months	1, 3, and 7 days	12	<1–~3/turbine/yr	Jain et al. 2009d
Clinton, NY	1.5 MW (67/23)	119	Flashing red (31/15)	6 months	1, 3, and 7 days	9	Not estimated	Jain et al. 2009c
Ellenburg, NY	1.5 MW (54/18)	119	Flashing red (17/5)	6.5 months	1, 3, and 7 days	7	Not estimated	Jain et al. 2009b

TABLE 1. Continued.

Location	Turbine type (total/study)	Turbine height (m)	Lighting type (total/study)	Study duration	Search interval during migration	Observed nocturnal migrant fatalities/yr	Estimated fatalities/turbine/yr	Reference
Madison, NY	1.65 MW (7/7)	100	Flashing red (7/7)	1 year	7–10 days	5	~1–2/turbine/yr	Kerlinger 2002b
Maple Ridge, NY	1.65 MW (195/50–64)	122	Flashing red (~60/17–18)	2 years	7 days	32	~2–4/turbine/yr	Jain et al. 2009a, b
Garrett, PA	1.3 MW (8/8)	90	Flashing red (8/8)	1 year	7–10 days	0	<1/turbine/yr	Kerlinger 2001
Buffalo Mountain I, TN	0.66 MW (3/3)	88	Flashing white (3/3)	3 years	0.5 weeks	15.7	~7/turbine/yr	Nicholson et al. 2005
Buffalo Mountain II, TN	0.66–1.8 MW (18/18)	88–120	Flashing white and flashing red (9/9)	1 year	7 days	5	~2/turbine/yr	Fiedler et al. 2007
Searsburg, VT	0.55 MW (11/11)	59	None	5 months	3–7 days	0	<1/turbine/yr	Kerlinger 2002a
Mountaineer, WV	1.5 MW (44/44)	105	Flashing red (12/12)	8 months	1 week	30[a]	~3/turbine/yr[a]	Kerns and Kerlinger 2004
Mt. Storm, WV	2.0 MW (82/27)	118	Flashing red (27/12)	6 month	1–7 days	36	~2–4/turbine/yr	Young et al. 2009
Eastern Canada								
Erie Shores, ON	1.5 MW (66/66)	119	Steady red (41/41)	2 years	3–24 days	~20	~1–2/turbine/yr	James 2008
Exhibition Place, ON	0.75 MW (1/1)	94	Flashing red (1/1)	11 weeks	0.5 weeks	2	~3–4/turbine/yr	James and Coady 2003
Piekering, ON	1.8 MW (1/1)	117	Flashing red (1/1)	1 year	3–7 days	2	~3–4/turbine/yr	James 2004

[a] A multi-bird fatality event caused by sodium-vapor lamps at a substation was exeluded from this analysis.

TABLE 2. Night migrant mortality comparison at lit and unlit turbines; wind farms with flashing red lights only. Lit-unlit column represents the difference between numbers of actual carcasses found at lit vs. unlit turbines, on a per turbine basis.

Location	Lit turbines			Unlit turbines			Lit-unlit	Reference	Statistical test, significance
	# lit turbines	# carcasses found at lit turbines	Observed fatalities per turbine	# unlit turbines	# carcasses found at unlit turbines	Observed fatalities per turbine	Difference in fatalities per turbine		
Western U.S.									
High Winds, CA	26	10	0.385	64	21	0.328	0.06	Kerlinger et al. 2006	Chi-square test, ns
Klondike, OR	9	0	0.000	7	4	0.571	−0.57	Johnson et al. 2003	Statistical test not reported
Stateline, OR/WA, 2002	39	9	0.231	85	23	0.271	−0.04	Erickson et al. 2004	Statistical test reported, $P > 0.10$, ns
Stateline, OR/WA, 2003	46	4	0.087	107	34	0.318	−0.23	Erickson et al. 2004	Statistical test reported, $P > 0.10$, ns
Nine Canyon, WA	15	3	0.200	22	3	0.136	0.06	Erickson et al. 2003	Overlapping 95% CI, ns
Judith Gap, MT	7	1	0.143	13	3	0.231	−0.09	TRC Env. Corp. 2008	Statistical test not reported
Central U.S.									
Ainsworth, NE	24	4	0.167	12	4	0.333	−0.17	Derby et al. 2007	Statistical test not reported
Kewaunee, WI	20	4	0.200	11	3	0.273	−0.07	Howe et al. 2002	Statistical test not reported
Eastern U.S.									
Mars Hill, ME, 2007	10	10	1.000	18	12	0.667	0.33	Stantec 2009	Statistical test not reported
Mars Hill, ME, 2008	10	7	0.700	18	8	0.444	0.26	Stantec 2009	Statistical test not reported
Clinton, NY, 2008, three-day searches	5	3	0.600	3	1	0.333	0.27	Jain et al. 2009c	Chi-square test, ns
Clinton, NY, 2008, weekly searches	5	1	0.200	2	2	1.000	−0.80	Jain et al. 2009c	Chi-square test, ns
Bliss, NY, 2008, daily searches	2	3	1.500	6	7	1.167	0.33	Jain et al. 2009d	Chi-square test, ns
Maple Ridge, NY, 2006, daily searches	3	24	8.000	7	34	4.857	3.14	Jain et al. 2007	Chi-square test, $0.10 > P > 0.05$, marginal significance
Maple Ridge, NY, 2006, weekly searches	7	2	0.286	23	18	0.783	−0.50	Jain et al. 2007	Chi-square test, ns
Maple Ridge, NY, 2007	18	7	0.389	46	18	0.391	0.00	Jain et al. 2009a	Chi-square test, ns
Maple Ridge, NY, 2008	17	14	0.824	47	25	0.532	0.29	Jain et al. 2009b	Chi-square test, ns
Mountaineer, WV	12	9	0.750	31	22	0.710	0.04	Kerns and Kerlinger 2004	Statistical test not reported
Mt. Storm, WV, daily searches	4	6	1.500	5	11	2.200	−0.70	Young et al. 2009	Overlapping 90% CI, ns
Mt. Storm, WV, weekly searches	8	7	0.875	10	5	0.500	0.38	Young et al. 2009	Overlapping 90% CI, ns

were often on site for 2–5 days/week because it required several days for turbines at a site to be searched. On-site technicians and maintenance staff at most wind farms were instructed to report avian fatalities, increasing the likelihood of recording large scale collision events at towers that were not part of the study.

We report both the raw numbers of night-migrant carcasses found during each study and estimates of fatalities/turbine/year. Most studies calculated estimates of fatalities/turbine/year from raw numbers of carcasses found, searcher efficiency tests or estimates, carcass removal (scavenging) tests or estimates, and area adjustments if the entire area beneath a turbine could not be searched. We used rates from studies in similar habitats to estimate fatalities likely/turbine/year for studies where searcher efficiency and carcass removal rates were not measured empirically. We did not estimate fatality rates at three sites where large portions of migration seasons were not covered or where searcher efficiency and carcass removal rates could not be estimated. Our rationale for including raw, unadjusted fatality numbers was to provide a comparison of actual carcass finds to fatality estimates, and to permit comparison with communication tower studies, where corrections for carcass removal and searcher efficiency have rarely been used.

We compared the unadjusted number of night migrant fatalities/turbine/year at lit (flashing red) and unlit turbines from 12 of 30 wind farms (Table 2) using a non-parametric Wilcoxon signed-rank test (Wilcoxon 1945). We wished to ascertain whether a significantly greater number of wind farm studies reported more carcasses at lit turbines versus unlit turbines.

RESULTS

Eight wind farms were examined in the western United States, seven in the central region, 12 in the eastern region, and three in Canada (Table 1). Two studies were reported for Buffalo Mountain, Tennessee because the type of lighting changed when the wind farm was expanded and larger turbines were installed. The number of turbines at these sites ranged between one and 454 and the number of turbines studied ranged from one to 153. Turbine nameplate production ranged from 0.4 to 2.0 MW, and turbine height ranged from 54 to ~125 m. Obstruction lighting was present at 28 of 30 wind farms studied. The percentage of turbines equipped with lighting ranged from ~25–33% (n = 22 studies) to 100% (n = 7 studies). Lighting on most illuminated turbines was flashing red lights (mainly L-864), but a few sites had steady-burning red (L-810), and two sites had flashing white lights (L-865). More than one type of lighting was used at four sites. Study durations ranged from >3 months to 5 years. There was variation in search interval among studies. We estimate the total number of individual turbine searches for all studies combined to be ~25,000 during spring and fall migration seasons.

Incidence of Multi-bird Fatality Events.—The number of carcasses found in the studies ranged from zero to 36/year, but when the number of turbines studied was considered, the average at turbines ranged from zero to ~5/turbine/year. Only four studies reported multi-bird fatality events (defined as >3 birds killed in one night at one structure), but they were at turbines with lighting other than flashing red or at turbines with ancillary, non-FAA-type lighting. Fourteen freshly-killed birds (11 warblers, 2 flycatchers, and 1 vireo) were recovered on 19 May 1999 at two adjacent turbines in a section of the wind farm at Buffalo Ridge in southwestern Minnesota (Johnson et al. 2000) where every other turbine was lit with steady-burning red lights. This event may have been related to a severe thunderstorm that occurred the night before the carcasses were discovered. This was the only multi-bird fatality event reported at the Minnesota site during 4 years of study.

Two multi-bird fatality events (3 fatalities at turbine # 2 on 10 Oct 2000, 7 fatalities at turbine # 3 on 31 Oct 2002) were recorded at Buffalo Mountain I in Tennessee (Nicholson et al. 2005) where each of three turbines had a pair of flashing white lights. The 10 October 2000 mortality event occurred during clear, cold, windy conditions following passage of a strong cold front, and the 31 October 2002 mortality event occurred during mild, rainy weather.

About 27 night-migrating passerines were found dead on the morning of 23 May 2003 at Mountaineer in West Virginia (Kerns and Kerlinger 2004) in the vicinity of three turbines and an electrical substation that was brightly lit at night by at least four sodium-vapor lamps (steady-burning white flood lights). Heavy fog occurred the night before this fatality event was discovered by maintenance workers, who alerted searchers. Seventeen of the fatalities were discovered at turbine # 23, which was ~50 m from the substation, five at the substation (collisions with

fencing), and three and two respectively at the flanking turbines, # 22 and 24, which were ~250 and 125 m, respectively from the substation. No further multi-bird fatality events occurred at the substation and adjacent turbines, including foggy nights, after the sodium-vapor lamps were extinguished. Few fatalities were found at searched turbines throughout the study, including those that had flashing red lights.

Comparison of Lit and Unlit Turbines at Same Site.—The FAA does not recommend that all turbines at a wind farm be lit, but we were able to test whether disproportionate numbers of fatalities occurred at turbines with obstruction lighting. There were two sites at which none of the turbines was lit and seven at which all of turbines were lit (Table 1). The two completely unlit sites had 0.55–0.60 MW turbines in the 59–61 m height range, and estimated fatality rates of <1 night migrant/turbine/year. Sites where all turbines were lit had 0.66–1.65 MW turbines in the 79–117 m height range, and estimated fatality rates of <1 to ~7 night migrants/turbine/year. Sites in eastern North America reported slightly greater estimated fatality rates (Table 1). This appeared to be the case for turbines of roughly equal height. Wind farms (n = 22) with both lit and unlit turbines had 0.36–2.00 MW turbines in the 54–125 m height range. Estimated fatalities ranged from <1 to ~4 birds/turbine/year with greater rates in eastern North America. Absolute numbers of fatalities were sufficiently large at 13 of 22 sites to make quantitative comparisons of fatality rates at lit and unlit turbines (Table 2). The rates were roughly the same at sites with flashing red lights, but may have been slightly greater at turbines lit with steady-burning red lights. We did not find that a significantly greater proportion of wind farm studies (Table 2) reported greater numbers of fatalities at lit turbines versus unlit turbines than expected by chance (Wilcoxon sign-rank test, n = 20, Z = 0.18, P = 0.43). This lack of evidence of a consistent trend with respect to fatality rates at lit versus unlit turbines across North America indicates it is highly unlikely flashing red lights are associated with greater fatalities. All but one of the studies reviewed that tested for differences in fatality rates at lit and unlit turbines reported no significant differences. The one exception was at Maple Ridge in New York, where a marginally significant difference was reported ($0.10 > P > 0.05$) in one of two statistical tests.

No significant differences in collision mortality were reported at wind farms with lit and unlit turbines where some or all lit turbines had other than flashing red lights. These included Crescent Ridge, Illinois (Kerlinger et al. 2007), Buffalo Ridge, Minnesota (Johnson et al. 2000, 2002), and Buffalo Mountain, Tennessee (Fiedler et al. 2007). Unadjusted mortality at Erie Shores, Ontario (James 2008), where all lit turbines had steady-burning red lights, was four times greater at lit than at unlit turbines (0.4/turbine vs. 0.1/turbine). The unadjusted rates, when turbines along the shore of Lake Ontario were removed from the calculations, were similar (0.35/turbine at lit vs. 0.28/turbine at unlit).

DISCUSSION

Collision fatality data from 30 wind farms in North America demonstrate that fatality rates of night migrating birds at these structures are relatively low, ranging between ~1 to 7/turbine/year. A comparison of estimated fatalities by geographic region showed a gradient with fatalities increasing from western to eastern North America. This mirrors continent-wide studies of bird migration patterns (Lowrey and Newman 1966, Gauthreaux et al. 2003) that show the density of migration in central and eastern states is greater than recorded in western states.

What is striking about the data from wind farms is the relative absence of large-scale fatality events, similar to those recorded at tall communication towers supported by guy wires, where collisions of hundreds of birds at times occur in a single night (Avery et al. 1980, Kerlinger 2000). Only four incidents (<0.02% of searches) were reported of multi-bird fatality events at wind turbines (n = >3 carcasses at a single turbine on a single night) during ~25,000 turbine searches in all studies combined. That so many studies and so many searches have been conducted at wind turbines without recording large-scale fatality events strongly suggests the probability of large-scale fatality events occurring is extremely low. Far more systematic research has been conducted at wind turbines than at communication towers or other structures, which supports the finding that large-scale fatality events rarely occur at wind turbines.

We believe there are three reasons why large-scale fatality events apparently do not occur at wind turbines and why fatality rates at wind turbines are much lower than has been reported for communication towers. First, communication

towers at which large-scale fatality events and large numbers of fatalities have been reported are taller than wind turbines. Wind turbines have rarely exceeded 125 m in height (this study), while communication towers for which large-scale fatalities have been found largely exceed 150 m and often exceed 305 m (Avery et al. 1980, Shire et al. 2000). Thus, communication towers extend into altitudes where more night migrants fly (Kerlinger and Moore 1989), than do wind turbines. Second, all communication towers for which large numbers of night migrant fatalities and large-scale events have been noted have guy wires (Shire et al. 2000), whereas wind turbines do not.

The third reason for higher fatality rates and large-scale fatality events at communication towers opposed to wind turbines may be related to the types of lights that are placed on communication towers and wind turbines. A majority of communication towers equipped with aviation obstruction lights have both steady-burning red (L-810) lights and flashing red (L-864) lights (FAA 2000). Wind turbines are most often equipped with only flashing red (L-864) lights (FAA 2000). The four multi-bird fatalities at single (or adjacent) turbines during a single night occurred at turbines with flashing white lights, steady-burning red lights, or ancillary facility lighting (sodium vapor lamps). Flashing red lights were not implicated in these multi-bird fatality events at turbines.

Gehring et al. (2009) recently demonstrated for communication towers that steady-burning red lights attract night migrants, but flashing red lights do not. Gehring et al. (2009) also demonstrated towers at heights ranging from 116 to 146 m, supported by guy wires and equipped with only flashing red lights, experienced 50–70% fewer fatalities than towers with both flashing and steady burning red lights. The average fatality rate was 17.5 carcasses found per 40 days of peak migration (20 days in spring and 20 days in fall) per communication tower with both flashing and steady-burning red lights. The estimated fatality rate at these towers, when adjustments for searcher efficiency and carcass removal by scavengers is included (equal to about a 2-fold increase; Gehring et al. 2009), is likely to be as high as 70 night migrants/tower/year when adjustments were made to include the entire spring and fall migration seasons. Gehring et al. (2009) reported 74 carcasses/40 days of searching/year (spring and fall seasons) without carcass removal or searcher efficiency adjustments at towers >305 m in height with guy wires. Adjustments for carcass removal and searcher efficiency, as well as adjustments that include the entire spring and fall migration seasons, increased these estimates to ~300 birds/tower/year. Thus, communication towers equipped with guy wires and a combination of flashing and steady-burning red lights have fatality rates that are one to two orders of magnitude greater than wind turbines.

We strongly suggest that reported fatalities of night-migrating birds are minimal at wind turbines based on results reported for communication towers (Gehring et al. 2009), especially when compared to tall, communication towers with guy wires. Note that Smallwood et al. (2010) estimated mortality at wind turbines was greater when novel scavenger removal methods were used. We did not find evidence that large-scale fatality events occur at wind turbines or that the flashing red lights normally used on wind turbines cause large numbers of fatalities of night migrants. Our results, combined with those reported by Gehring et al. (2009), strongly suggest that wind turbines be equipped only with flashing red lights (strobe or LED) and that steady burning red lights not be used on turbines. It is prudent that post-construction fatality studies continue at wind turbines, especially those taller than those we report, and at turbines erected in geographic areas where studies have not been conducted and greater numbers of birds may migrate.

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DEVELOPMENTAL CHANGES IN SERUM ANDROGEN LEVELS OF EASTERN SCREECH-OWLS (*MEGASCOPS ASIO*)

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ABSTRACT.—We studied androgen production during development in nestling Eastern Screech-Owls (*Megascops asio*) and hypothesized that gender and hatch order might influence serum levels of testosterone and androstenedione. Testosterone levels were highest immediately after hatching and declined significantly in the 4 weeks leading to fledging. The average level of testosterone for 1–7 day-old owls was 3.99 ± 0.68 ng/ml. At 22–28 days of age, the average testosterone level for nestling owls was 0.83 ± 0.18 ng/ml. Testosterone levels did not differ between males or females. The average testosterone level for male nestlings was 2.23 ± 0.29 ng/ml and 2.39 ± 0.56 ng/ml for female nestlings. The average level of androstenedione for nestling owls was 1.92 ± 0.11 ng/ml and levels remained constant throughout development. Levels were significantly higher in males than females. The average androstenedione level was 1.77 ± 0.16 ng/ml for male nestlings and 1.05 ± 0.24 ng/ml for female nestlings. Hatching order did not affect levels of either androgen. Our results provide a foundation for future studies of androgen production by nestling owls. *Received 19 January 2010. Accepted 30 June 2010.*

Androgens influence many aspects of adult bird physiology and behavior, including metabolic rate (Hannsler and Prinzinger 1979), lipid storage (Wingfield 1984), timing of molt (Runfeldt and Wingfield 1985), song production (Hunt et al. 1997), and aggression (Hau et al. 2000). Androgens also influence the behavior of nestling birds, as testosterone levels in earlier-hatching White Stork nestlings (*Ciconia ciconia*) and Tawny Owl nestlings (*Strix aluco*) are correlated with elevated aggression towards siblings (Sasvári et al. 1999, 2006). Testosterone enhances the probability of aggressive behavior in young Domestic Chickens (*Gallus gallus domesticus*) (Young and Rogers 1978) and facilitates aggression in Black-headed Gull chicks (*Chroicocephalus ridibundus*) (Groothuis and Meeuwissen 1992, Ros et al. 2002). Testosterone also facilitates begging behavior in nestling Atlantic Canaries (*Serinus canaria*) (Buchanan et al. 2007) and European Pied Flycatchers (*Ficedula hypoleuca*) (Goodship and Buchanan 2006).

Sex steroids are present early in avian development and are important in sexual differentiation. Testicular hormone synthesis in Domestic Chicken embryos has first been detected on day 6 of incubation, and peaks in plasma levels of testosterone occur on day 14 (Woods and Weeks 1969). Similarly, androgen production begins on day 8 of incubation in embryos of male Japanese Quail (*Coturnix japonica*), and androgen concentrations in plasma reach a plateau before hatching (Ottinger and Bakst 1981, Schumacher et al. 1988). Less is known concerning the maturation of the hypothalamic-pituitary-gonadal (HPG) axis in altricial birds. Sex steroids are present in the plasma of altricial hatchlings of several species (Hutchison et al. 1984, Adkins-Regan et al. 1990, Schlinger and Arnold 1992, Silverin and Sharp 1996). However, the typical levels of androgens produced by nestling birds, whether androgens are produced primarily in the gonads or the adrenal glands, or how these levels change through development have not been studied in detail. Many field studies sample individuals only once (e.g., Fargallo et al. 2007, Gil et al. 2008). However, a number of studies suggest that circulating androgen levels can vary during development. Testosterone levels of nestling Great Tits (*Parus major*) decline significantly during development (Silverin and Sharp 1996), and circulating androgen levels initially increase, then decrease post-hatching in nestling Zebra Finches (*Taeniopygia guttata*) (Adkins-Regan et al. 1990).

Evidence concerning differences between male and female nestlings varies among species. Male and female Common Kestrel (*Falco tinnunculus*) (Fargallo et al. 2007), European Pied Flycatchers (Goodship and Buchanan 2006), Zebra Finches (Naguib et al. 2004), and nestling Lesser Black-backed Gulls (*Larus fuscus*) (Verboven et al. 2003) show no difference in circulating androgen levels. However, nestling male Black Coucals

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(*Centropus grillii*) have higher levels of circulating androgens than females (Goymann et al. 2005), and nestling female Atlantic Canaries (Weichel et al. 1986) and Japanese Quail (Ottinger et al. 2001) have higher levels of circulating androgens than males.

Hormonal differences have also been reported among nestlings in regards to hatching order and may be due to social interactions (Wingfield et al. 1990). Second-hatching chicks were shown to have higher levels of circulating testosterone 1 day after hatching, as well as during aggressive encounters with older siblings in obligately siblicidal Nazca Boobies (*Sula granti*) (Ferree et al. 2004). First-hatched White Stork nestlings are more aggressive, receive more food, and have higher plasma levels of testosterone than their siblings (Sasvári et al. 1999). Similarly, plasma testosterone levels decreased with hatching order in 3-day-old Tawny Owls raised by females in poor condition. Owlets raised by females in good condition, however, had similar levels of testosterone, regardless of hatching order (Sasvári et al. 2006). Hatching order in other species is not related to plasma androgen levels (Naguib et al. 2004).

We describe developmental patterns of androgen production by Eastern Screech-Owls (*Megascops asio*) during the nestling phase. Androgens, including testosterone and androstenedione, are produced primarily by the gonads. The adrenal glands are also a source of androgens, specifically androstenedione and dehydroepiandrosterone (DHEA), but production is minimal compared to the gonads. Most androgenic effects are mediated by testosterone and dihydrotestosterone. Androstenedione also circulates in the bloodstream at relatively high levels, but it has a significantly lower affinity for the androgen receptor compared to testosterone and dihydrotestosterone, and a relatively low biological activity *in vivo*. Instead, androstenedione serves primarily as a substrate for the production of testosterone and estrogens (Hadley and Levine 2007). Several studies have characterized levels of testosterone in nestling birds (Fargallo et al. 2007, Gil et al. 2008), but little is known about typical serum levels or developmental patterns of androstenedione.

We measured serum testosterone and androstenedione levels weekly in captive nestling Eastern Screech-Owls from hatching until fledging. Our objectives were to: (1) characterize levels of testosterone and androstenedione produced by nestling owls, (2) compare how these levels changed during the developmental period between hatching and fledging, (3) ascertain whether levels differ between male and female nestlings, and (4) whether levels differ among nestlings in regard to hatching order.

METHODS

Species and Study Area.—The Eastern Screech-Owl is a small owl (males are typically 160 g, females 200 g) with a distribution that extends east of the Rocky Mountains and south from the Canadian boreal forest to the Tropic of Cancer in Mexico (Gehlbach 1994). Clutches normally consist of 4–6 eggs; the first 2–3 eggs are laid 1 day apart with increasing intervals afterwards (Gehlbach 1994). Onset of incubation varies among females and depends on environmental conditions, but may begin with the first, second, or third egg. Incubation typically lasts 28 days; eggs hatch asynchronously over 2–3 days, and sibling feeding hierarchies are established. The young fledge between 28 and 30 days of age (Gehlbach 1994).

The owls used in this study are part of a captive colony of breeding birds maintained at Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland, USA. Owls are fed two mice per bird daily and Nebraska Bird of Prey Diet fortified with Vionate. They are housed in 12 × 3 m outdoor flight cages that contain nest-boxes, and pairs are kept together year-round. Egg-laying begins in March. Females solely incubate, and males provide food to incubating females and nestlings after hatching.

Serum Collection and Androgen Assays.—Fifty-two blood samples were collected weekly during spring 2007 from 26 nestlings in nine clutches. Samples were collected only from nestlings hatching from first-laid clutches, and nestlings hatched between 28 April and 13 May 2007. Individual owls ranged from 2 to 27 days of age, and clutches contained 2–5 nestlings. Seven owl nestlings were sampled once, 12 were sampled twice, and 7 were sampled three times. No birds were sampled more that three times during the 4 weeks of blood collection. Serum samples were obtained by venipuncture from the brachial vein using a 27-gauge needle until the last week before fledging, when they were taken from the jugular vein using a 25-gauge needle. A separate blood sample was also taken for identification of males and females just before fledging. Serum samples

were frozen until shipped to the St. Louis Zoo for hormone analysis.

Serum samples were transferred to 2-ml eppendorf tubes and diluted 1:2 with phosphobuffered saline (PBS). Samples were mixed with a vortex and an equal volume of 100% ethanol was added to precipitate proteins and lipids following Kozlowski and Ricklefs (2010). Samples were immediately homogenized upon adding ethanol and allowed to incubate at room temperate for 10 min. Samples were then spun at 12,282 *g* in a centrifuge for 10 min. The supernatant was poured into a sterile cryule tube and frozen at −70° C until an assay was performed.

All samples were analyzed using radioimmunoassay (RIA) in the Endocrinology Laboratory at the St. Louis Zoo. Ethanol extracts were thawed and spun in a centrifuge at 12,282 *g* for 10 min to remove any remaining lipids in preparation for assay. Testosterone and androstenedione concentrations were measured using commercially available coated-tube radioimmunoassay kits (Coat-A-Count © Total Testosterone 125I Kit, and Coat-A-Count © Direct Androstenedione 125I Kit, Diagnostic Products Corporation, Los Angeles, CA, USA). The lowest detection limit was 0.05 ng/ml and upper limit was 40 ng/ml in the testosterone assay. The lowest detection limit of the androstenedione assay was 0.04 ng/ml and the upper detection limit was 8.7 ng/ml. Both kits used in this study have highly specific antibodies. The testosterone antibody cross-reacts as follows: 5β-androstan-3α, 17β-diol: 0.4%; androstenedione: 0.5%; 5β-androstan-3β, 17β-diol: 0.2%; 5α-dihydrotestosterone: 3.3%; 5(10)-estren-17α-ethinyl-17β-ol-3-one: 0.2%; 4-estren-17α-methyl-17β-ol-3-one: 1.1%; 4-estren-17-ol-3-one: 20%; 19-nortestosterone: 20%; ethisterone: 0.7%; 19-hydroxyandrostenedione: 2.0%; 11-ketotestosterone: 16%; methyltestosterone: 1.7%; norethindrone: 0.1%; 11β-hydroxyyestosterone 0.8%; and triamincinolone: 0.2%. The androstenedione antibody cross-reacts as follows: androsterone: 0.14%; DHEA: 0.16%; progesterone: 0.16%; spironolactone: 0.11%; 5α-dihydrotestosterone: 0.21%; and testosterone: 1.49%. Cross-reactivities for all other compounds are below 0.1%.

Assays were conducted following kit directions with the exception that kit standards, which are supplied in human serum, were replaced by standards diluted in 10% steroid-free calf serum. Standard diluent was added to extracted serum samples, and steroid-free owl serum extract was added to standards and quality controls to equalize the matrices of standards and samples. Owl serum extract and calf serum were stripped of steroids using dextran-coated charcoal (DCC# 6241, Sigma Chemical, St. Louis, MO, USA) prior to use. All samples were analyzed in the same assay in duplicate for both testosterone and androstenedione. Mean ± SE intra-assay variation of duplicate samples was 8.96 ± 1.21 for testosterone and 9.66 ± 2.42 for androstenedione.

Assay Validation.—We added a known amount of radioactively labeled hormone to a serum sample before extraction to measure extraction efficiency of both testosterone and androstenedione, and measured the amount of radioactivity after the extraction process. Serum was pooled from the experimental samples and divided into 10 samples, each containing 15 μL of serum. In five samples each for testosterone and androstenedione, 15 μL of I-125 labeled hormone and 15 μL of PBS were added to the 15 μL of serum. Control samples consisted of 15 μL of labeled hormone and 30 μL of PBS. Two samples of 15 μL of I-125 hormone were set aside to measure the total radioactivity present in the sample. Serum and control samples were extracted as described, and the supernatant was transferred from each sample to an individual 12 × 75 plastic test tube. The total amount of radioactivity in each sample was measured in both serum and control samples, and compared to the total count tubes to calculate the recovery percentage in each sample. Percent recovery was 91–97% for both hormones and did not differ between control and serum samples (testosterone: $t = 1.22$, df = 8, $P = 0.26$; androstenedione: $t = 0.73$, df = 8, $P = 0.49$).

Four samples that contained high levels of hormone were diluted by 1/2, 1/4, and 1/8 with steroid-free owl serum extract for both testosterone and androstenedione. Serial dilutions of extracted serum samples were parallel to the standard curve (test of equal slopes, $P > 0.34$ for testosterone; $P > 0.29$ for androstenedione) (Zar 1999), supporting that no additional substances in the extract were cross reacting with the antibody. We assessed the accuracy of both assays by adding a known amount of either testosterone or androstenedione to four serum extracts containing low values of hormone. Addition of known amounts of the androgens at two dosage levels resulted in recovery of 101 ± 3.6% of added testosterone and 96 ± 2.9% for androstenedione.

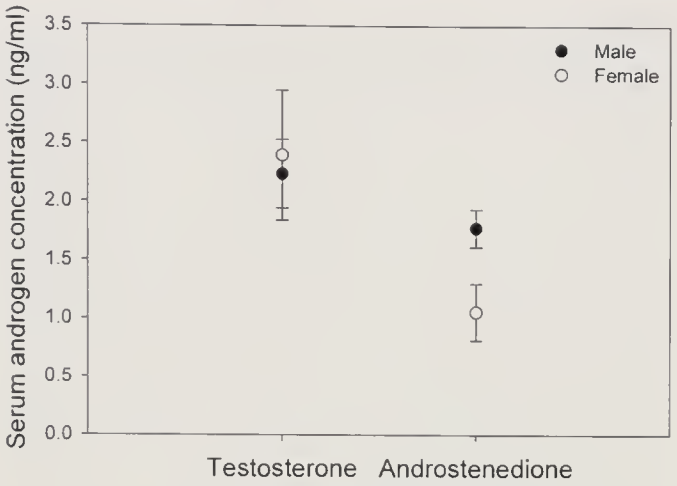

FIG. 1. Concentration ($\bar{x}$ ± SE) of testosterone and androstenedione in the serum of male and female Eastern Screech-Owl nestlings (n = 19 males, 7 females).

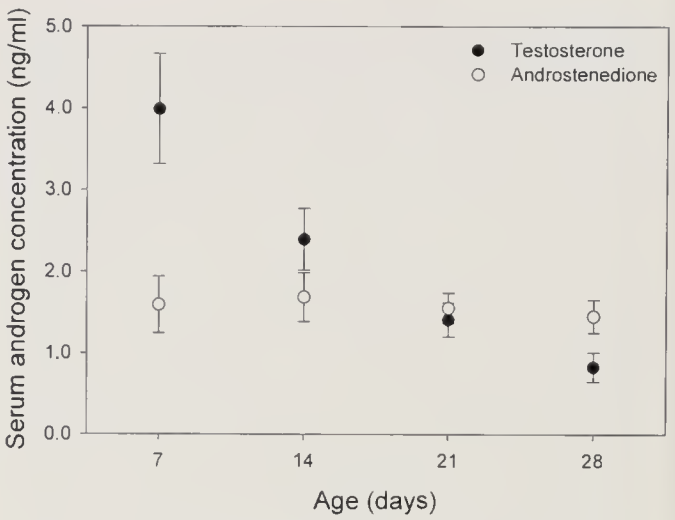

FIG. 2. Weekly concentration (± SE) of testosterone and androstenedione in the serum of Eastern Screech-Owl nestlings: n = 12 nestlings in age-class 1; n = 18 nestlings in age-class 2; n = 17 nestlings in age-class 3; n = 5 nestlings in age-class 4.

Identification of Males and Females.—We followed Griffiths et al. (1998) to identify each individual nestling Screech-Owl as male or female by amplifying introns of the genes CHD-W and CHD-Z through PCR.

Statistical Procedures.—All statistical analysis was conducted using JMP 7.0.2 © (SAS Institute 2008). Blood samples were collected weekly, and nestlings were not sampled on the same day during each week; thus, nestlings were divided into 7-day age classes. These classes ranged from 1–7 to 22–28 days of age. General Linear Models were used to assess the relationship between testosterone and androstenedione in relation to age-class, hatch-order, brood size, and male/female. A separate analysis was conducted for each androgen. Nest of origin and individual owl were treated as random effects. Hatch-order, male/female, brood size, and all two-way interactions were included as fixed effects. Non-significant fixed effects were dropped from the model. A Tukey HSD test was used to separate means when results were significant.

RESULTS

Both testosterone and androstenedione were detected in the serum of nestling Screech-Owls. The average concentration of testosterone in nestling owls was 2.30 ± 0.26 ng/ml and levels ranged from 0.17 to 7.59 ng/ml. The average concentration of androstenedione was 1.92 ± 0.11 ng/ml and ranged from 0.98 to 3.51 ng/ml.

Testosterone and androstenedione levels were unaffected by both brood size and hatch-order, and these effects were dropped from both statistical models. Seven of the nestlings in our study were females, and 19 were males. No differences in serum testosterone were observed between male and female nestlings ($F_{1,46}$ = 0.68, P = 0.41). Average testosterone levels were 2.23 ± 0.29 ng/ml for male nestlings and 2.39 ± 0.56 ng/ml for female nestlings. In contrast, serum androstenedione levels differed significantly between male and female nestlings. Male owls had higher levels of androstenedione than females ($F_{1,46}$ = 5.173, P = 0.030). Average androstenedione levels were 1.77 ± 0.16 ng/ml for male nestlings and 1.05 ± 0.24 ng/ml for female nestlings (Fig. 1).

Testosterone levels did not differ between male and female nestlings, and the data were pooled for analysis. Nestling testosterone concentrations declined with age ($F_{3,46}$ = 11.489, P < 0.001) (Fig. 2). In contrast, androstenedione levels did not vary by age for either male ($F_{3,46}$ = 1.58, P = 0.21) or female ($F_{3,46}$ = 0.37, P = 0.78) nestlings. Testosterone levels were higher than androstenedione levels during the 2 weeks following hatching. However, by weeks 3 and 4, testosterone and androstenedione were present at similar levels. Average testosterone levels in chicks 1–7 days of age measured 3.99 ± 0.68 ng/ml. By week 4 (days 22–28), levels declined to less that one-quarter of their initial level, to 0.83 ± 0.18 ng/ml. Androstenedione concentrations averaged 1.72 ± 0.38 ng/ml for 1–7 day old male nestlings and 1.01 ± 0.65 ng/ml for 1–7 day old female nestlings. Average androstenedione levels by 22–28 days of age were 1.39 ± 0.15 ng/ml for males and 1.25 ± 0.58 for females.

DISCUSSION

Testosterone and androstenedione are both measurable in nestling Screech-Owl serum from week 1 post-hatching until fledging. Our results demonstrate both a significant change in the level of testosterone during development and a difference in the pattern of testosterone and androstenedione during development. Testosterone is highest during the first week following hatching, and then declines. Androstenedione levels remain relatively constant from hatching through fledging.

The HPG axis has been studied in detail in precocial species, but less is known about hormone production by altricial nestlings. The ovary and testes actively produce steroid hormones, including testosterone, during early embryonic development through post-embryonic development in precocial Domestic Chickens (Tanabe et al. 1979) and Mallards (*Anas platyrhynchos*) (Tanabe et al. 1983). The adrenal glands also appear to be important for androgen synthesis in precocial species. Testosterone is found at high concentrations in the adrenal gland shortly before hatching in both Domestic Chickens (Tanabe et al. 1979) and Mallards (Tanabe et al. 1983).

Developmental studies of the HPG axis in altricial species are restricted to passerines. Limited work suggests the HPG axis of these species matures later in development. Silverin and Sharp (1996) demonstrated the hypothalamus and pituitary gland in Great Tits become functional 9 days after hatching, approximately halfway through their nestling phase. Injections of GnRH at this age elicit increases in male testosterone or female estradiol. The adrenal gland may also be an important source of androgens for altricial nestlings. Castration of nestling Zebra Finches did not significantly reduce plasma androgen levels, suggesting these androgens may arise primarily from the adrenal gland (Adkins-Regan et al. 1990). Our study suggests nestling Screech-Owls are capable of producing measureable levels of both testosterone and androstenedione. However, whether these androgens are gonadal or adrenal is unknown. Further study is needed to ascertain if development of the HPG axis in other altricial species, including owls, is similar to passerine species.

We found a decrease in nestling testosterone levels during post-hatching development similar to other studies (Adkins-Regan et al. 1990, Silverin and Sharp 1996). Testosterone levels in Great Tit nestlings are highest in newly hatched birds, and reach basal levels by 3 days of age (Silverin and Sharp 1996). Male Zebra Finches have higher levels of plasma testosterone during days 2–14 of development than in older nestlings (Adkins-Regan et al. 1990). Similarly, Schlinger and Arnold (1992) found male Zebra Finches had higher levels of plasma androgens at 7–9 days of age compared to 4–6-day-old birds or 10–13-day-old birds. Elevated testosterone levels are also characteristic of the period surrounding hatching in several precocial species, including Japanese Quail (Ottinger and Bakst 1981, Schumacher et al. 1988) and Domestic Chickens (Tanabe et al. 1979). This suggests testosterone may have a role in hatching. In contrast, androstenedione levels of nestling owls did not vary during post-hatching development. Androstenedione levels of precocial species change during development, but little is known about developmental patterns in altricial nestlings. Androstenedione levels in Domestic Chickens are elevated in pre-pubescent males (Culbert et al. 1977), and then decrease between 9 and 16 weeks of age when testicular maturation occurs (Sharp et al. 1977). Whether similar changes occur during nestling owl development is unknown.

We found no differences in testosterone levels between male and female nestling Screech-Owls at any stage of development. This is similar to the findings for several other species (Groothuis and Meeuwissen 1992, Verboven et al. 2003) including Common Kestrels (Fargallo et al. 2007). In contrast, we detected a difference in androstenedione level, as male Screech-Owls had higher levels of androstenedione than females from hatching through fledging. There is limited evidence that male nestlings of other species may also maintain higher levels of androstenedione than females. Male European Starling (*Sturnus vulgaris*) nestlings have been shown to produce higher levels of DHEA (a precursor of androstenedione) than female nestlings (Chin et al. 2008). Elevated levels of testosterone in nestling birds have been correlated with behavioral changes, including enhanced aggression (Sasvári et al. 1999, 2006), and begging intensity (Goodship and Buchanan 2006). However, it is unknown whether higher levels of androstenedione in male nestlings would produce similar effects. Androstenedione has a much lower affinity for the androgen receptor compared to testosterone and a relatively low biological activity (Hadley and Levine 2007). Whether higher levels of androstenedione in male nestlings have any physiological effects is unknown.

Hatching order was not associated with differences in androgen levels in nestling Screech-Owls. The correlation between hatching order and serum androgens can be associated with the presence of sibling feeding hierarchies. First-hatched nestlings in several species have higher plasma levels of testosterone, are more aggressive, and receive more food than younger siblings (Sasvári et al. 1999, 2006). Sibling feeding hierarchies are often established in wild Screech-Owl broods, and nestlings vigorously compete for food resources (Gehlbach 1994). However, the owls in this study were from a captive colony where they have an abundant food supply. High androgen levels are known to be immunosuppressive and reduce growth for nestlings, in addition to increasing their aggressive behavior (Ros 1999, Fargallo et al. 2007). We have observed that captive owl nestlings show little sibling competition, and lack of a correlation between androgens and hatching order may be associated with reduced competition. Future work will characterize the androgen levels of Screech-Owl nestlings when food resources are restricted. This will allow us to ascertain if androgen levels are affected by hatching order when there is strong sibling competition among siblings for food.

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STRESS RESPONSIVENESS DECREASES WITH AGE IN PRECOCIAL, JUVENILE CHUKAR

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ABSTRACT.—Development of the hypothalamic-pituitary-adrenal (HPA) axis and subsequent corticosterone (CORT) release in newly hatched birds is a balance between limiting exposure to the detrimental effects of CORT on growth and development, and the necessity of mounting an acute stress response. We measured the stress responsiveness of juvenile Chukar (*Alectoris chukar*) 20 to 60 days post-hatch prior to molting into full adult plumage. The integrated CORT response during 60 min of restraint in these individuals decreased with age. Comparisons to mean adult integrated CORT values imply the youngest juveniles have greater responses than adults while the oldest juveniles have reduced CORT responses. This pattern is currently an anomaly within the altricial-precocial range and suggests specific tradeoffs, such as molting into adult plumage, may affect timing of HPA suppression during development. *Received 23 November 2009. Accepted 20 April 2010.*

The acute stress response in adult animals is an adaptive physiological reaction to noxious stimuli and is hallmarked by release of glucocorticoids following a hormone cascade along the hypothalamic-pituitary-adrenal (HPA) axis (Sapolsky et al. 2000). Corticosterone (CORT) is the predominant glucocorticoid secreted in avian species and, after CORT is released into the system, negative feedback mechanisms act to quickly shut down CORT secretion (Dallman and Bhatnagar 2001). Excessive CORT release, either due to a disrupted HPA axis or altered negative feedback sensitivity, can lead to physiological and behavioral pathologies (McEwen 2005). Glucocorticoids, in terms of development, have severe effects on growth as they promote muscle breakdown; elevated concentrations of glucocorticoids lead to muscle wasting and decreased growth rates (Wingfield 1994, Morici et al. 1997, Sapolsky et al. 2000). In addition, glucocorticoid concentrations can affect key aspects of neuronal development in the central nervous system (Sapolsky and Meaney 1986). Elevated CORT can also affect feather development (Romero et al. 2005, DesRochers et al. 2009).

Development of the HPA axis and the stress response system in young birds post-hatch is considered to be a delicate balance between benefiting from the ability to mount an acute stress response and limiting the damaging effects of glucocorticoids. This balance requires tight regulation due to the impact of glucocorticoids on growth and feather development (Walker et al. 2005, Wada et al. 2007). Altricial laboratory rodents display a clear and easily defined "stress hyporesponsive period" or SHRP, beginning 2 days postnatal (reviewed by Sapolsky and Meaney 1986). A hyporesponsive period has also been noted in many altricial and semi-altricial avian species including Magellanic Penguins (*Spheniscus magellanicus*) (Walker et al. 2005), White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) (Wada et al. 2007), Northern Mockingbirds (*Mimus polyglottos*) (Sims and Holberton 2000), American Kestrels (*Falco sparverius*) (Love et al. 2003), Slender-billed Prions (*Pachyptila belcheri*) (Quillfeldt et al. 2009), and Atlantic Canaries (*Serinus canaria*) (Schwabl 1999). Hatchlings were shown to be fully capable of mounting an adult-like response within days of hatching by precocial species including Mallards (*Anas platyrhynchos*) (Holmes et al. 1990), chickens (*Gallus gallus domesticus*) (Freeman 1982), and Domestic Turkeys (*Meleagris gallopavo*) (Wentworth and Hussein 1985), and in semi-precocial Great-winged Petrels (*Pterodroma macroptera*) (Adams et al. 2008) and the semi-altricial Snowy Owl (*Bubo scandiacus*) (Romero et al. 2006).

The HPA response, in most studies of altricial and semi-altricial avian species, slowly increases with age and fledglings about to leave the nest are close to adult-like responses (Schwabl 1999, Love et al. 2003, Walker et al. 2005, Blas et al. 2006, Wada et al. 2007). Chickens, a precocial species, show a clear but short hyporesponsive period immediately following hatching (Freeman 1982). However, there are limited data on development of the stress response in precocial species that match studies tracking development of the stress-response system in altricial species.

Our objective was to measure the stress responsiveness of juvenile Chukar (*Alectoris chukar*), within an age range in which they were

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post-hatch but had yet to develop full adult plumage, to track the pattern of their HPA development.

METHODS

Study Species.—Chukar are non-migratory desert-adapted ground birds. They were introduced into North America from the steep, arid mountains of southwestern Eurasia as game birds, and can now be found extensively throughout the arid mountains of the American west (Christensen 1996). We captured wild juvenile and adult Chukar from a remote region of the Mojave Desert within the U.S. Navy China Lake Naval Air Weapons Station (CLNAWS) near Ridgecrest, California (117° 37′ W, 36° 3′ N). Limited human access into CLNAWS assured minimal, non-experimental human interaction with our population. Juvenile Chukar in desert environments can be relatively easy to capture due to limited dispersal during summer months and faithfulness to a specific water source (Larsen et al. 2007).

Chukar are precocial and leave the nest with their mother immediately after hatching, and are fully capable of flight within 2 weeks of hatching (Christensen 1996). We trapped Chukar at human-made rainwater catchments known as ''guzzlers'' and one spring-fed pool from mid-July to August in 2006 and 2008. The guzzler system and trapping technique at CLNAWS have been described (Delehanty et al. 2004).

Field Procedures.—We weighed Chukar immediately upon capture and used the absence of a full black collar and eye band coloration as an indication of their juvenile status (Christensen 1996). We captured 31 juvenile Chukar with body mass ranging from 115 to 390 g. Juveniles representing the range of masses were captured evenly across the sampling period. These masses, according to the growth chart in Pis (2003), indicate juveniles were between 20 and 60 days of age. Adults in this region are, on average, 500 g (based on raw data collected for Dickens et al. 2009a, b; Fig. 1). Juveniles typically reach adult size at ~12 weeks of age (Christensen 1996). Our study was limited by method of capture and time period in which it was conducted. We did not obtain samples from chicks immediately post-hatch as we were not following nests, and trapping began within a period in which most chicks were at least a few weeks of age.

Capture-Stress Protocol.—Birds captured were provided with shade, *ad libitum* water, and were removed from the trap within 3 hrs of entering. Time spent in the trap was not ideal and we previously justified this experimental methodology (Dickens et al. 2009a). All individuals for which we were able to obtain baseline samples (samples taken within 3 min of approaching the trap, $n = 27$) demonstrated baseline samples well below their respective peak restraint-induced CORT concentrations, and all baseline concentrations were within the range expected for this species.

We sampled CORT responsiveness of all individuals by placing them into an opaque bag and taking blood samples at 15, 30, and 60 min to measure the capacity for an endocrine stress response. All animal use complied with AALAC guidelines and was approved by the Tufts Institutional Animal Care and Use Committee. CORT was measured using radioimmunoassay (RIA) (Wingfield et al. 1992) as previously used for this species (Dickens et al. 2009a, b).

Statistical Analysis.—We calculated the relative total CORT release over the 60-min restraint period as an integrated CORT value using measurements at 15, 30, and 60 min (Romero 2004). This measurement allowed us to compare the overall capacity of the HPA axis to release CORT over the 60-min restraint period. We performed a regression comparing each individual's integrated CORT versus their mass (GraphPad, Prizm 4b). We also analyzed a group of adults sampled upon first capture from the wild to compare adult mass and the adult stress responsiveness. We present these results as means ± SE (subset of data reanalyzed from that in Dickens et al. 2009a, b).

RESULTS

We found a correlation between body mass and integrated CORT concentrations that was significantly different from zero (Fig. 1; $r^2 = 0.32$, $P < 0.001$) for the 31 juveniles captured and sampled. Adult Chukar ($n = 19$), captured during the same years as the juveniles, had a mean integrated CORT response of 2,188.0 ± 142.5 ng/mL/min and a mean body mass of 453.3 ± 12.2 g. There was no correlation between adult mass and integrated CORT concentrations ($r^2 = 0.002$, $P = 0.904$).

DISCUSSION

CORT response decreased with age in the precocial Chukar for the age range investigated

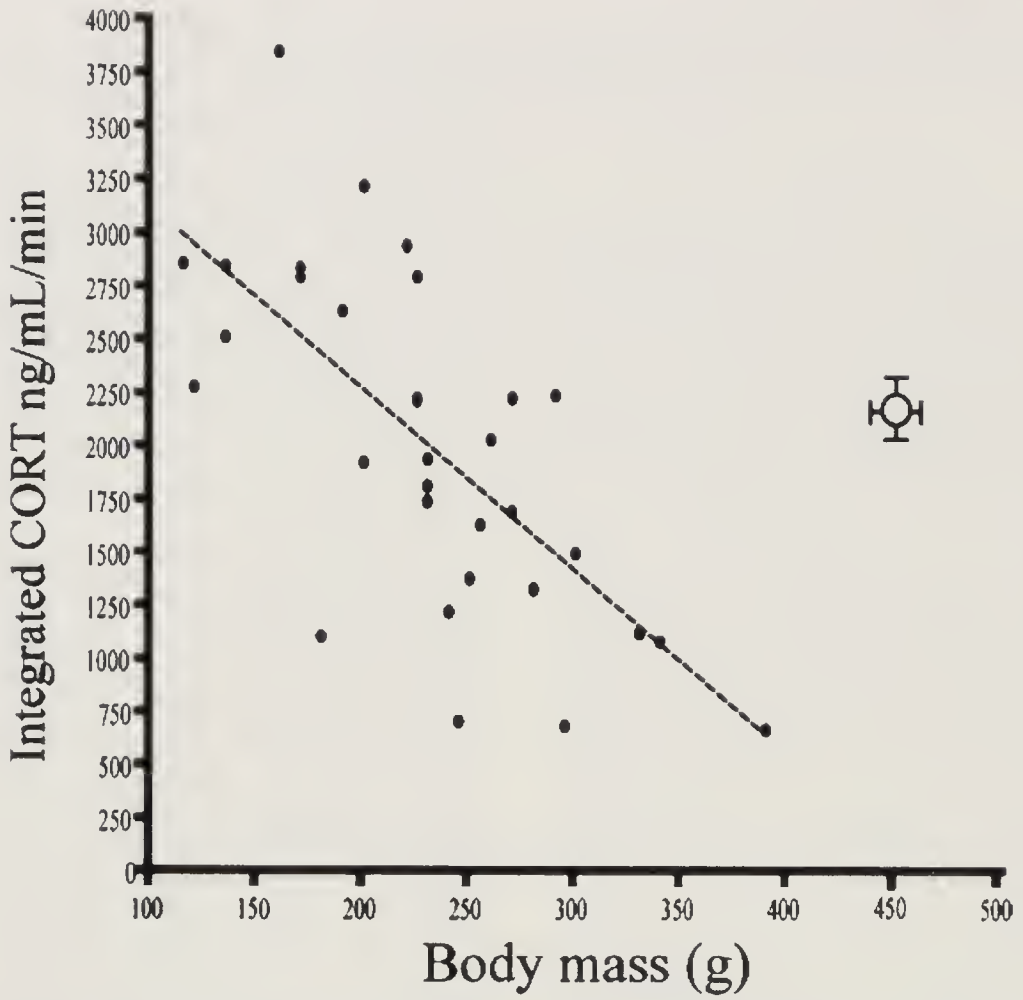

FIG. 1. Individual points (n = 31) represent a single juvenile's integrated CORT measurement versus body mass. The regression line is significantly different from zero ($r^2 = 0.32$, $P < 0.001$). The open circle represents the adult mean values ± SE for each parameter (n = 19).

and the heaviest, oldest, birds had the lowest response. The average adult response was in the middle of the juvenile response range. The youngest birds had relatively higher stress responses than adults while the oldest juveniles, closest to full maturity, had a relatively lower response than that of adults.

This pattern contrasts to that observed in altricial and semi-altricial species for which the HPA response becomes more similar to adult-like responses as the nestlings reach fledging (e.g., Love et al. 2003, Walker et al. 2005, Wada et al. 2007). The slow development of the HPA response in these altricial species fits well with the developmental hypothesis summarized by Blas et al. (2006). Altricial species are either completely dependent or substantially dependent on parents for all aspects of their lives (Ricklefs 1979). They are also completely constrained to the nest and their capacity to escape a stressor, such as a predator, is extremely limited. Having an HPA response to an inescapable stimulus would lead to elevated CORT concentrations and do more harm to their growth and development than good for their recovery from the stressor (Blas et al. 2006).

Precocial young, in contrast, are out of the nest and exposed to the same stressors as adults. Precocial juveniles of a variety of species are as fully capable of a quick escape from a predator as are adults (Herrel and Gibb 2004) and, for Chukar, all major requirements for quick flight escape occur within 8 days post-hatch (Jackson et al. 2009). Juveniles can physically escape as well as adults, and it also seems likely they initiate an adult-like CORT response. Obtaining an adult-like response early in life is the pattern observed in the limited studies that investigate precocial young. There is a hyporesponsive period in chickens immediately following hatch but chicks are able to mount a full CORT response within the first day (Freeman 1982). Full responsiveness by the semi-precocial Great-winged Petrel was measured after hatch and chicks remained responsive throughout the juvenile period (Adams et al. 2008). However, Mallard duckling responses,

immediately after hatch, were more robust and actually decreased to match the adult response by day 21 (Holmes et al. 1990). We also observed a more robust response by younger than older juvenile Chukar. We were not able to sample individuals earlier than 20 days after hatch and do not know whether Chukar hatchlings show some hyporesponsive period immediately after hatch similar to altricial species. We also cannot discuss the potential HPA response profile of the birds during this earlier developmental stage. However, the striking difference that our data confirm is that precocial young can have an adult or an even greater CORT response within a few weeks of hatching.

The capacity of the juvenile Chukar response appears to decrease beyond the adult response as they become older. These data imply a hidden tradeoff in elevating CORT concentrations during the late part of the juvenile stage. Preventing excessive CORT exposure outweighs the benefits of having the capacity for an adult CORT response. The tradeoff may reflect continued growth during this time, although the rate of growth is less than in younger juveniles (Pis 2003). Alternatively, successful molting of juvenile feathers to grow adult feathers during this time may be sufficiently important to trump full HPA responsiveness. Chukar begin prebasic molt at 5 weeks of age, and the molt is nearly complete by 16 weeks (Christensen 1996). CORT concentrations, both baseline and stress-induced concentrations, are low during seasonal molt in adults (Romero and Remage-Healey 2000). Elevated CORT concentrations can lead to decreased protein deposition in feathers (Romero et al. 2005) and, perhaps as a result, reduced feather quality (DesRochers et al. 2009). Juveniles are ~250 g in mass at 5 weeks of age (the time of Prebasic molt according to Christensen 1996), if we extrapolate age from mass in the graph provided by Pis (2003), this age relates to the point at which the line (Fig. 1) decreases below the adult average. Older juveniles are growing adult flight feathers and replacing other body feathers to form the black band and collar typical of this species. Elevated CORT concentrations in Barn Owl (*Tyto alba*) chicks can lead to decreased deposition of pigment in growing feathers (Roulin et al. 2008). Maintaining low CORT during this period of feather replacement may be important for not only building strong adult flight feathers but also for acquiring appropriate adult coloration.

More research is necessary to ascertain whether this pattern of HPA responsiveness is unique to Chukar, present in precocial species in general, or present only in precocial species that have distinct adult coloration patterns. This pattern is currently an anomaly in the growing literature investigating how the HPA develops within altricial-precocial species and may help understand the specific tradeoffs that affect when birds should suppress HPA responsiveness or express full adult-like responses.

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Short Communications

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Composition Dynamics of an Avian Assemblage

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ABSTRACT.—I summarize the 10-year composition dynamics of a riparian avifauna on the Arapaho National Wildlife Refuge, Colorado, USA. Only 15 of the 89 breeding bird species (19,393 individuals) were present each of the 10 years whereas 25 species were only recorded in a single year. Number of species in any given year ranged from 30 to 57 (34 to 64% of the 10-year cumulative species total). The number of species detected >1 and <10 years represented over half of all species with no pattern of either increasing or decreasing across years of study. Short-term definitions of species richness preclude the ability to define the major dynamic within an avian assemblage—species that use the site an intermediate number of years. Understanding the ecological prerequisites for these species should provide greater insight into current physical habitat and climate changes occurring on-site. *Received 16 February 2010. Accepted 24 June 2010.*

Ornithologists have historically inventoried a local avifauna to define the biological significance of an area: the more species present, the presumed greater ecological diversity and conservation significance of the locale. The number of species present is often referred to as species richness, or alpha diversity when viewed from broader spatial scales (Knopf and Samson 1994). Ecological studies have used species richness to interpret avian responses to changes in landscapes resulting from either natural processes or management practices (Conroy and Noon 1996, Brand et al. 2008, Johnson et al. 2009).

Annual variation in species richness and relative species composition define conservation significance of an area (Fleishman et al. 2006). However, among-year variation in species composition is generally ignored and the number of species recorded across the 2–4 years of most studies is often presented as a single number to define conservation significance. Species immigration and emigration are assumed to be equal in such studies, although data addressing this assumption are notably lacking.

I noted that species composition within an avian assemblage varied annually while species richness remained comparatively stable during a 10-year study of the breeding-bird assemblage in a shrub willow (*Salix* spp.) association along the Illinois River in the Arapaho National Wildlife Refuge, 1980–1989. The patterning of composition change was much more dynamic than the standard assumption that individuals of some species colonize an area as individuals representing other species leave. I briefly summarize the 10-year composition dynamics of avifaunal change with the intent to discourage use of species richness derived from short-term studies in assessments of conservation significance or efficacy of management actions at local sites.

METHODS

My coworkers and I studied the breeding bird assemblage along the Illinois River floodplain within the Arapaho National Wildlife Refuge (ANWR), Jackson County, Colorado, USA, from 1980 through 1989. The refuge is at an elevation of 2,485–2,516 m, within an intermountain glacial basin of upland vegetation dominated by sagebrush (*Artemisia* spp.). The riparian shrub assemblage comprises species of willows (*Salix bebbiana*, *S. caudata*, *S. exigua*, *S. geyeriana*, *S. monticola*, *S. planifolia*, *S. pseudocordata*, and *S. wolfii*) that grow to heights of 6 m (Cannon and Knopf 1984). Photographs of the study area are in Knopf et al. (1988: 281) and Sedgwick and Knopf (1992:724).

We inventoried the breeding bird assemblage annually in the latter half of June, well after spring migrants had left ANWR. Each year, two observers each surveyed bird species and individuals at 200 (185 in 1980) points spaced at 100-m intervals (to reduce visual overlap between survey points) along each side and at random distances perpendicular to the river bank. The survey was conducted from the stream bank where the willow stand was less than 20 m wide. The radius of the

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TABLE 1. Number of bird species recorded on 400, 10-min survey plots along the Illinois River floodplain on the Arapaho National Wildlife Refuge, Colorado, 1980–1989.

Year	No. species	No. individuals
1980[a]	30	1,079
1981	35	1,231
1982	50	1,867
1983	45	1,841
1984	57	2,309
1985	45	1,866
1986	45	1,955
1987	43	2,154
1988	42	2,225
1989	57	2,866
1980–1989	89	19,393

[a] Sampling effort was 370 plots in 1980.

survey circle was not restricted to allow detection of larger, wary species.

Avian surveys were conducted from one-half hour before sunrise until 1000 hrs MDT each morning except in periods of inclement weather. An observer moved to each survey point, waited 1 min and then recorded the species of each bird detected within the following 10-min interval. Each observer participated in multiple years of the surveys.

RESULTS

We detected 1,079–2,866 individuals representing 30–57 avian species during surveys of the Illinois River floodplain in any given year, 1980 through 1989 (Table 1). Cumulative totals of 19,393 individuals representing 89 species were recorded across the 10-year period. The number of species recorded in any specific year ranged from 34 to 64% of the collective number of species recorded across the 10-year period.

Detection of a given species in the floodplain also varied among years (Table 2). Only 15 (17%) of the cumulative 89 species were seen in all 10 years. Many more, 25 (28%), species were seen in only one of the 10 years. The number of detections within a species, ranged from >4,000 Yellow Warblers (*Dendroica petechia*) (Buckland et al. 1993) to a single record for many species that were only recorded in 1 year.

Over half (49 of 89, 55%) of the species recorded on ANWR were present >1 but <10 years. The number of species detected in an intermediate number of years showed neither a clear pattern of increasing nor decreasing with increasing years of study.

DISCUSSION

Ten of the 89 species present within the floodplain were waterfowl reflecting the management objective of ANWR to enhance breeding habitats for waterfowl by promoting taller herbaceous vegetation to encourage nesting. Six raptor species foraged within the floodplain although most nested off the study area. Most cavity-nesting species did not have on-site nest substrates, but did forage as a part of the breeding

TABLE 2. Number of years a species was recorded on 400, 10-min survey plots along the Illinois River floodplain on the Arapaho National Wildlife Refuge, Colorado, 1980–1989.

No. years[a]	No. species	Species[b]
10	15	AMRO, BBMA, BCCH, BHCO, BRBL, GWTE, LISP, RWBL, SASP, SOSP, WCSP, WEME, WIFL, WISN, YEWA
9	7	AMGO, GADW, HOWR, KILL, MALL, YHBL, WIPH
8	3	AMWI, BCNH, MODO
7	6	CITE, COGR, CONI, NOFL, SPSA, SWHA
6	8	BWTE, AMCR, COYE, FOSP, LESC, NOSH, TRSW, VEER
5	4	BASW, BRSP, NOPI, SORA
4	6	AMCO, GBHE, GTTO, NOHA, SEOW, WIWA
3	9	AMKE, BEKI, DUFL, GHOW, PISI, REDH, SWTH, VESP, WAVI
2	6	CAGO, CLSW, GRCA, MAWR, RCKI, GRSG
1	25	AMBI, BTHU, BUOR, CANV, CHSP, COFL, CORA, DOWO, EAKI, EUST, FOTE, GRHE, GRYE, HOLA, INBU, LABU, LEOW, OCWA, RNPH, RTHA, SATH, SSHA, VIRA, WEKI, YBCU

[a] Sampling effort was 370 plots in 1980.
[b] Species codes in the Appendix.

bird assemblage, as did Green-tailed Towhee (*Pipilo chlorurus*) and Sage Thrasher (*Oreoscoptes montanus*) that nested in the sagebrush uplands. Greater Sage-Grouse (*Centrocercus urophasianus*) were not known to nest within the floodplain, but occasionally moved broods into the riparian vegetation. Collectively, these species contributed a meaningful component to the species richness and conservation significance of the site, although the floodplain only provided one component of the habitat required for breeding.

Earlier studies on ANWR included both basic studies of single species, i.e., Yellow Warbler (Knopf and Sedgwick 1992, Howe and Knopf 2000) and Willow Flycatcher (*Empidonax traillii*) (Sedgwick and Knopf 1988, 1989, 1992), and applied studies of grazing-response guilds (Knopf et al. 1988, Stanley and Knopf 2002). Those studies focused on species that occurred at densities adequate to insure sample sizes to support statistically rigorous analyses—species that were present all 10 years. Their certain presence revealed these species were more tolerant of ecologic or climatic change occurring locally within the study area across the decade. Extending avian surveys on ANWR another 10 years would result in no increase in the number of species with >95% probability of appearance each year.

Twenty-five species were present only one of 10 years. These species were likely non-breeders as spring migrants had left the refuge before the late June surveys. Some individuals may have been post-breeding dispersers from other locales, whereas others were stragglers as they were well outside documented breeding ranges. Extending avian surveys on the ANWR another 10 years would increase the cumulative list of avian species for the site to 100 species or more across a 20-year period. This latter component of species richness is not 'rich' at all, but peripheral to any meaningful definition of the breeding bird assemblage or management actions on the ground.

Interpreting or monitoring the significance of an area for avian conservation using a list of species recorded during a short-term study is problematic in that one component of the assemblage (species present every year) is ecologically tolerant of subtle environmental changes and another component is only present incidentally. Declines or increases in numbers of both common and rare/accidental species would only be expected following relatively catastrophic changes in the landscape. The larger problem, however, is that short-term studies are unable to distinguish "incidental" species from those that periodically use the site during the breeding season. Research investigations focusing on the ecological prerequisites for species that use an area intermittently should provide greater insight into more subtle physical and climate changes that drive species habitats within a local avian assemblage. The ability to identify these species already exists where standardized protocols to monitor breeding birds have been in place for multiple years.

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APPENDIX. Alphabetical list of species codes (Table 2).

Code	Species
AMBI	American Bittern (*Botaurus lentiginosus*)
AMCO	American Coot (*Fulica americana*)
AMCR	American Crow (*Corvus brachyrhynchos*)
MAKE	American Kestrel (*Falco sparverius*)
AMGO	American Goldfinch (*Spinus tristis*)
AMRO	American Robin (*Turdus migratorius*)
AMWI	American Wigeon (*Anas americana*)
BASW	Barn Swallow (*Hirundo rustica*)
BBMA	Black-billed Magpie (*Pica hudsonia*)
BCCH	Black-capped Chickadee (*Poecile atricapillus*)
BCNH	Black-crowned Night-Heron (*Nycticorax nycticorax*)
BEKI	Belted Kingfisher (*Megaceryle alcyon*)
BHCO	Brown-headed Cowbird (*Molothrus ater*)
BRBL	Brewer's Blackbird (*Euphagus cyanocephalus*)
BRSP	Brewer's Sparrow (*Spizella breweri*)
BTHU	Broad-tailed Hummingbird (*Selasphorus platycercus*)
BUOR	Bullock's Oriole (*Icterus bullockii*)
BWTE	Blue-winged Teal (*Anas discors*)
CAGO	Canada Goose (*Branta canadensis*)
CANV	Canvasback (*Aythya valisineria*)
CHSP	Chipping Sparrow (*Spizella passerina*)
CITE	Cinnamon Teal (*Anas cyanoptera*)
CLSW	Cliff Swallow (*Petrochelidon pyrrhonota*)
COFL	Cordilleran Flycatcher (*Empidonax occidentalis*)
COGR	Common Grackle (*Quiscalus quiscula*)
CONI	Common Nighthawk (*Chordeiles minor*)
CORA	Common Raven (*Corvus corax*)
COYE	Common Yellowthroat (*Geothlypis trichas*)
DOWO	Downy Woodpecker (*Picoides pubescens*)
DUFL	Dusky Flycatcher (*Empidonax oberholseri*)
EAKI	Eastern Kingbird (*Tyrannus tyrannus*)
EUST	European Starling (*Sturnus vulgaris*)
FOSP	Fox Sparrow (*Passerella iliaca*)
FOTE	Forster's Tern (*Sterna forsteri*)
GADW	Gadwall (*Anas strepera*)
GBHE	Great Blue Heron (*Ardea herodias*)
GHOW	Great Horned Owl (*Bubo virginianus*)
GRCA	Gray Catbird (*Dumetella carolinensis*)
GRHE	Green Heron (*Butorides virescens*)
GRYE	Greater Yellowlegs (*Tringa melanoleuca*)
GTTO	Green-tailed Towhee (*Pipilo chlorurus*)
GWTE	Green-winged Teal (*Anas crecca*)
HOLA	Horned Lark (*Eremophila alpestris*)
HOWR	House Wren (*Troglodytes aedon*)

APPENDIX. Continued.

Code	Species
INBU	Indigo Bunting (*Passerina cyanea*)
KILL	Killdeer (*Charadrius vociferus*)
LABU	Lazuli Bunting (*Passerina amoena*)
LEOW	Long-eared Owl (*Asio otus*)
LESC	Lesser Scaup (*Aythya affinis*)
LISP	Lincoln's Sparrow (*Melospiza lincolnii*)
MALL	Mallard (*Anas platyrhynchos*)
MAWA	MacGillivray's Warbler (*Oporornis tolmiei*)
MODO	Mourning Dove (*Zenaida macroura*)
NOFL	Northern Flicker (*Colaptes auratus*)
NOHA	Northern Harrier (*Circus cyaneus*)
NOPI	Northern Pintail (*Anas acuta*)
NOSH	Northern Shoveler (*A. clypeata*)
OCWA	Orange-crowned Warbler (*Vermivora celata*)
PISI	Pine Siskin (*Spinus pinus*)
RCKI	Ruby-crowned Kinglet (*Regulus calendula*)
REDH	Redhead (*Aythya americana*)
RNPH	Red-necked Phalarope (*Phalaropus lobatus*)
RTHA	Red-tailed Hawk (*Buteo jamaicensis*)
RWBL	Red-winged Blackbird (*Agelaius phoeniceus*)
GRSG	Greater Sage-Grouse (*Centrocercus urophasianus*)
SASP	Savannah Sparrow (*Passerculus sandwichensis*)
SATH	Sage Thrasher (*Oreoscoptes montanus*)
SEOW	Short-eared Owl (*Asio flammeus*)
SORA	Sora (*Porzana carolina*)
SOSP	Song Sparrow (*Melospiza melodia*)
SPSA	Spotted Sandpiper (*Actitis macularius*)
SSHA	Sharp-shinned Hawk (*Accipiter striatus*)
SWHA	Swainson's Hawk (*Buteo swainsoni*)
SWTH	Swainson's Thrush (*Catharus ustulatus*)
TRSW	Tree Swallow (*Tachycineta bicolor*)
VEER	Veery (*Catharus fuscescens*)
VESP	Vesper Sparrow (*Pooecetes gramineus*)
VIRA	Virginia Rail (*Rallus limicola*)
WAVI	Warbling Vireo (*Vireo gilvus*)
WCSP	White-crowned Sparrow (*Zonotrichia leucophrys*)
WEKI	Western Kingbird (*Tyrannus verticalis*)
WEME	Western Meadowlark (*Sturnella neglecta*)
WIFL	Willow Flycatcher (*Empidonax traillii*)
WIPH	Wilson's Phalarope (*Phalaropus tricolor*)
WISN	Wilson's Snipe (*Gallinago delicata*)
WIWA	Wilson's Warbler (*Wilsonia pusilla*)
YBCU	Yellow-billed Cuckoo (*Coccyzus americanus*)
YEWA	Yellow Warbler (*Dendroica petechia*)
YHBL	Yellow-headed Blackbird (*Xanocephalus xanocephalus*)

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A Digital Spot-mapping Method for Avian Field Studies

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ABSTRACT.—Avian mapping, also known as spot mapping or territory mapping, is a breeding season bird-survey technique that traditionally uses paper maps on which locations of birds are recorded. This method is often considered the most accurate in yielding a density, but has been criticized as being inefficient, time consuming, and inexact. We describe a novel digital-mapping method, incorporating a hand-held computer and high-accuracy global positioning system receiver (GPS), used in an ongoing boreal birds study. Digital mapping surpassed our expectations as to efficiency, flexibility, and work flow. We expect this method will become increasingly useful in many types of field studies, especially as costs decrease (currently ~$2,100 for the field receiver used). *Received 4 January 2010. Accepted 23 June 2010.*

Avian mapping, also known as spot mapping or territory mapping, is a widely used bird-survey technique in which an observer attempts to record the exact locations of individual birds within a defined study plot. The method emerged in the early 20th century as part of a naturalistic, observational approach to field biology, and was first described by Williams (1936:376) who wrote that "by the use of weekly maps ... it is possible to build up a series ... covering the nesting season, which will show concentrations of records about certain localities." Subsequent researchers expanded on Williams's idea and offered methods of statistical interpretation of mapping data (Kendeigh 1944, Pough 1947, Hall 1964). However, field methods for mapping in ornithology have remained essentially static since Robbins (1970) offered an international standard (Verner 1985, Manuwal and Carey 1991, Bibby et al. 2000).

The mapping method most commonly used involves establishment of a physical grid, 8–20 ha in size, using flagging or stakes to mark gridline intersections. An observer walks slowly along the gridlines noting the location of observed birds on a paper map using a set of symbols to indicate species, M/F, and behavior. The observer compiles the maps from each visit after 5–10 visits, creating one map per species. This enables delineation of individual birds' territories and estimation of breeding-bird density and diversity, as well as habitat structure and composition at bird locations or territories (Robbins 1970, Manuwal and Carey 1991, Ralph et al. 1993, Bibby et al. 2000).

The main limitations of the paper mapping field method as currently applied concern two areas: (1) the large time investment required for collecting and compiling data, and (2) the chances of making errors during data recording and interpretation. It can be time-consuming to create a physical grid using flagging and stakes over 8–20 ha, especially in thick vegetation or rough terrain. Compiling several maps for each bird species requires hours of data preparation and invites human error in interpreting and transferring data from one map to another. Recording detailed bird locations, behavior, and movements on maps scaled for practical field use can be inaccurate on paper maps (Verner and Milne 1990).

We studied habitat associations of lowland boreal birds in Adirondack Park, New York, USA with 10-min variable circular plot point counts in 2008. However, we decided that a more location-explicit approach was warranted for subsequent data collection after the initial field season. Our study was focused on a group of rare, cryptic birds in wet and often densely vegetated terrain. Thus, we sought a method that would provide more flexibility in detecting rare birds and allow us to spend more time at high-diversity sites than allowed by fixed-point counts. These requirements led us to use mapping as a technique for the 2009 field season. We suspected that paper-based mapping was not sufficiently efficient, accurate, or flexible for our needs and would be laborious to incorporate into our existing Geographic Information System (GIS). We (1) describe a novel

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TABLE 1. Target species of lowland boreal bird study, Spring Pond Bog, Adirondack Park, New York.

Species	Common name
Picoides arcticus	Black-backed Woodpecker
Contopus cooperi	Olive-sided Flycatcher
Empidonax flaviventris	Yellow-bellied Flycatcher
Perisoreus canadensis	Gray Jay
Poecile hudsonicus	Boreal Chickadee
Dendroica tigrina	Cape May Warbler
D. palmarum	Palm Warbler
D. castanea	Bay-breasted Warbler
Melospiza lincolnii	Lincoln's Sparrow
Euphagus carolinus	Rusty Blackbird

digital-mapping method that incorporates a high-accuracy global positioning system receiver (GPS), a hand-held computer, and a GIS-derived grid, and (2) discuss the advantages over traditional paper mapping as well as potential drawbacks.

METHODS

Our study area was the Spring Pond Bog Preserve, owned by The Nature Conservancy, in northern Adirondack Park, New York (44° 22′ 23″ N, 74 30′ 21″ W). We applied the digital-mapping method to our study of habitat associations of lowland boreal birds, a suite of 10 species that occur in the scattered lowland boreal habitats of the Adirondacks (Table 1). We established five 9-ha plots and visited each plot five times from 28 May to 8 July 2009, starting 15 min after sunrise.

We created a GIS prior to entering the field using ArcGis Desktop 9.2 (ESRI 2007) that contained orthographic aerial photographs, wetlands, roads, trails, and other geospatial data layers. We created five 300- × 300-m digital plots centered on point-count locations where we had recorded high target bird diversity in 2008. We divided each of these plots into a grid of 900 10- × 10-m squares (Fig. 1), and created a point layer for recording bird observations. We created drop-down menus for attributes such as date, species, seen/unseen, M/F, and behavior to facilitate data entry in the field (Fig. 2). We loaded these data layers into ArcPad 7.1 on a Trimble Nomad handheld computer. The Nomad was equipped with a Wide-Area Augmentation System (WAAS)-enabled Garmin 10X Bluetooth GPS receiver.

We conducted plot visits in much the same way as paper mapping. However, we used the Nomad along with a compass for navigation and data recording. We selected a random starting point and path through each plot by spinning a compass, and then proceeded at a calm, quiet pace through the plot using the Nomad's "Tracklog" feature to ensure that we followed grid lines so that we came within 20 m of every grid point. A full 9-ha plot visit lasted 90–120 min. No flagging or stakes were necessary to mark the plot or grid.

When we detected an individual of one of the target species, we ascertained its exact location and noted behavioral data related to territoriality or nesting activity. We then walked to the bird's location and, after ensuring the chosen GPS accuracy measure, Positional Dilution of Precision (PDOP), was below the pre-established threshold of 3.5, created a new data point using the Nomad touch screen. We decided on a PDOP threshold of 3.5 based on recommendations in the literature (i.e., Kennedy 2002) and expected accuracy under variable field conditions (from open, boggy peatlands with low relief to dense conifer wetlands). We used the drop-down menus in creating this point (Fig. 2) to record attributes of the detection. We changed the map view according to navigational or data-recording needs throughout the visit. For example, when locating an individual bird, we zoomed to a scale of ~1:400 (in which a grid square is 2.54 cm wide), whereas while navigating we used a scale of 1:1,000–2,000. For comparison, a typical paper map with a 9-ha grid would be scaled to 1:1,600 (in which a grid square is 0.64 cm wide). Each week we backed up the data set to our desktop GIS.

RESULTS

We recorded 153 individual detections of nine of the 10 target lowland boreal bird species in 25 plot visits. The number of target individuals detected per visit ranged from 3.8 to 10.2 ($\bar{x}$ = 6.12, σ = 2.44) while total target species recorded per grid ranged from 2 to 7 ($\bar{x}$ = 5.0, σ = 1.87). We compiled species detection maps for all sites after uploading the Nomad data to a desktop GIS (Fig. 1).

DISCUSSION

The digital spot-mapping method was easy to use and work flow efficiency exceeded our expectations for spatial and attribute accuracy, and data acquisition and storage speed. Drop-down menus made field data entry fast and

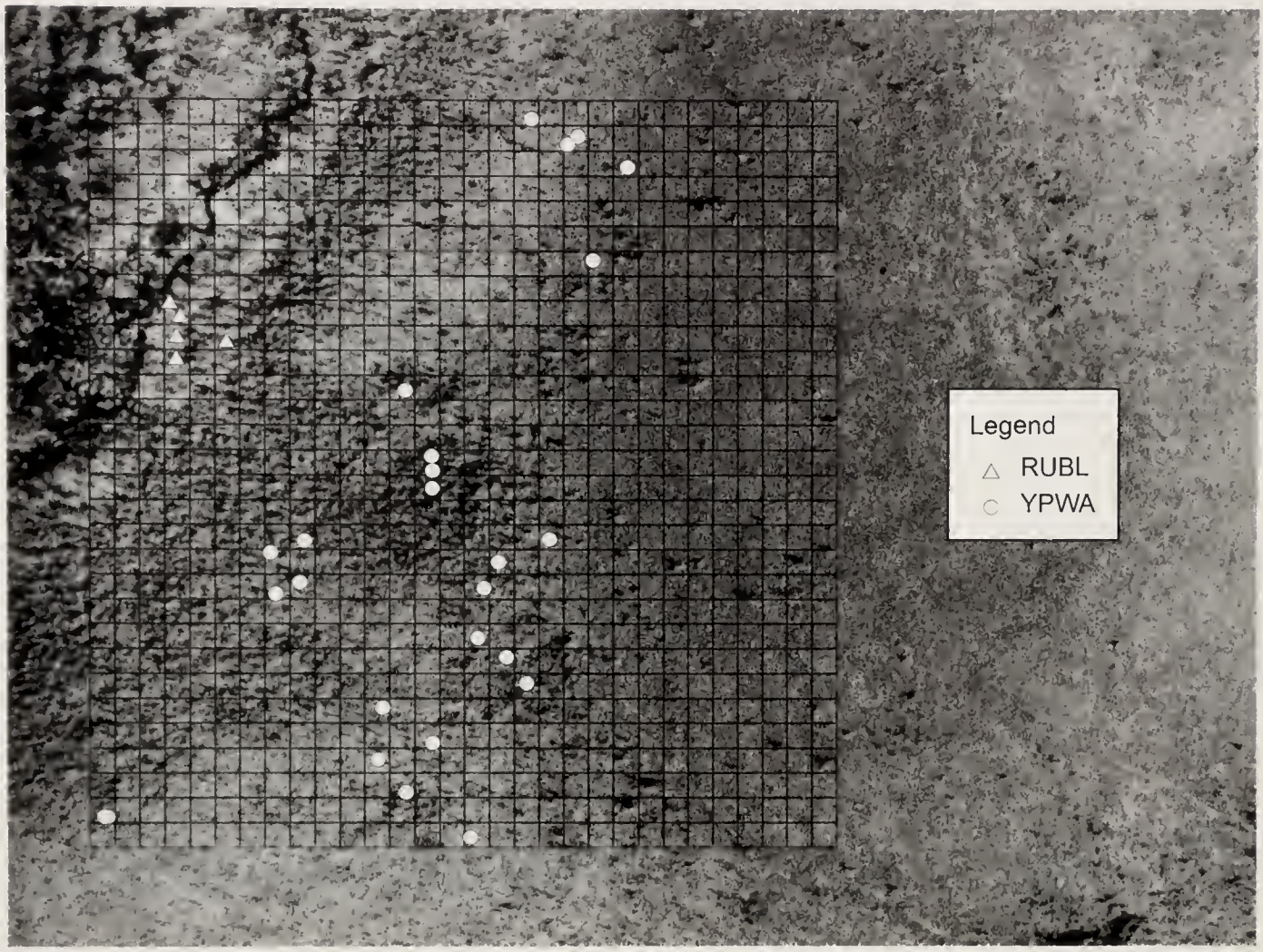

FIG. 1. Example of 300- × 300-m (9-ha) digital grid with accumulated detections of Rusty Blackbird (RUBL) and Palm Warbler (YPWA) at site SPB08, Spring Pond Bog, Adirondacks, New York.

unambiguous, unlike the complex system of paper map symbols an observer must correctly interpret to record breeding bird attributes. Dense or diverse bird populations can render paper mapping time-consuming and confusing, if not unusable. Digital mapping has no functional upper limit, as existing data points do not preclude recording additional observations at the same location. The map can be scaled in the field to show more or less detail, and dense bird populations can be recorded without clutter. Errors of translation can be substantially reduced, as there is no need to interpret and compile multiple paper maps, especially if that compilation occurs after the details of field observations fade from memory.

The Bluetooth GPS quickly and consistently obtained accurate locations, keeping us on the path of travel with no need to mark the plot in advance. The Nomad straps safely to one hand, enabling the observer to enter data, use binoculars, and navigate over obstacles and through wetlands while maintaining the travel path. Battery power lasted for ~20 hrs of field use. We kept the electronic devices charged with an AC adapter for our vehicle.

We did not directly compare the two methods but, in our experience, digital-mapping data can mirror data acquired by typical paper mapping studies. A review of recent studies that used the traditional mapping method (Fink et al. 2006, Toms et al. 2006, Villard et al. 2007, Romdal and Rahbek 2008, Gale et al. 2009) indicates that each could have incorporated digital mapping with little or no change to other aspects of the study while achieving a probable gain in efficiency in data acquisition and processing. Digital mapping can be also adapted to record unlimited additional data point attributes, whereas paper mapping would require additional data sheets for any additional data.

We encountered some problems with the digital-mapping method related to the specific combination of device–software interface. ArcPad

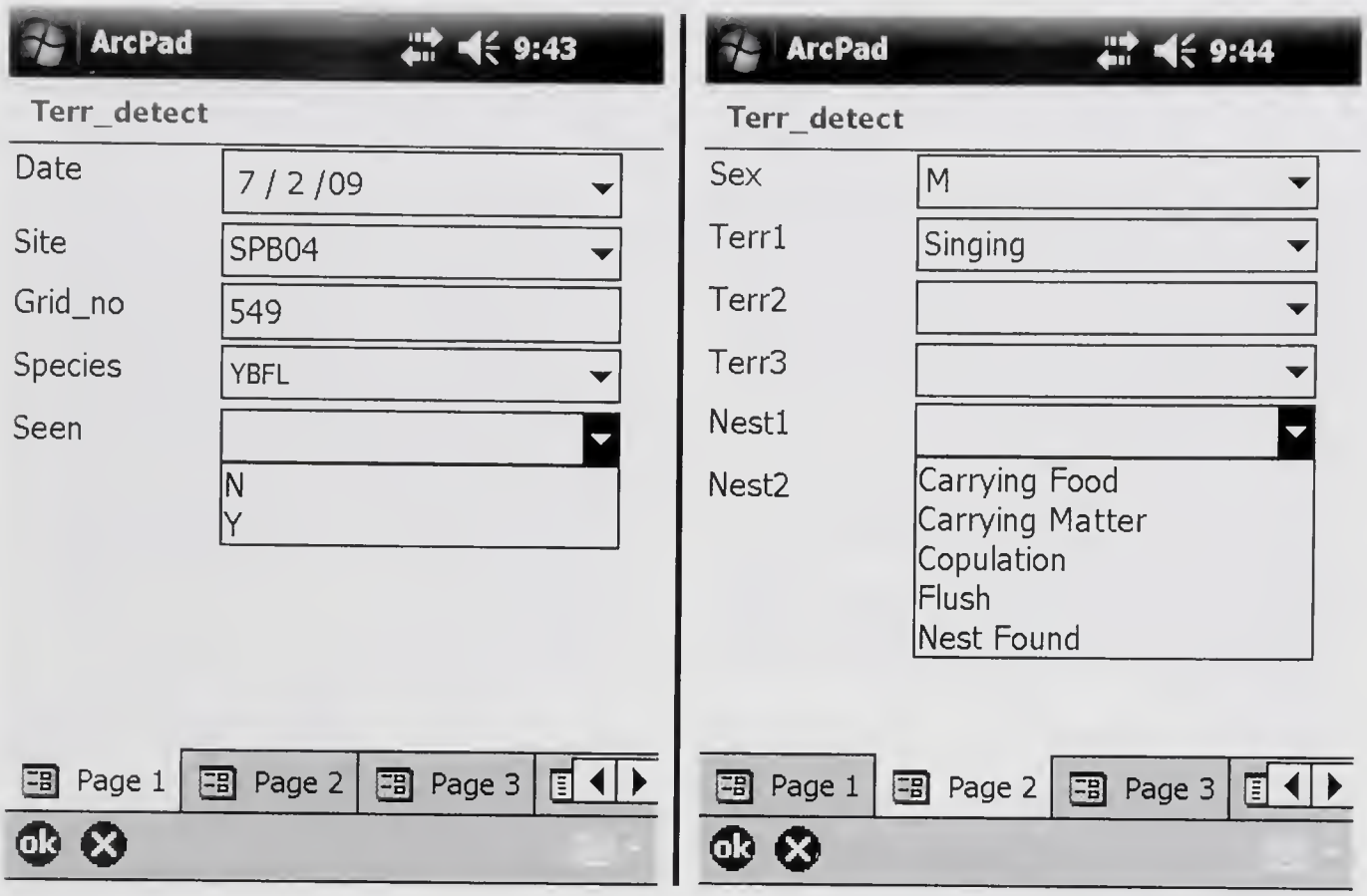

FIG. 2. Screenshot of Trimble Nomad running ArcPad 7.1 with drop-down menus used to enter data in lowland boreal bird mapping study, Spring Pond Bog, Adirondacks, New York.

7.1 is cumbersome to use in the field without access to an ArcGIS-equipped computer because changes to menus, data layers, or data sets must be made using ArcGIS. The operating system of the Nomad (Windows Mobile 6) hindered data processing, especially in customization and adding functionality. The interface between ArcGIS and ArcPad was limited, requiring us to download GIS shapefiles using Windows Sync rather than ArcGIS.

A second limitation of digital mapping is cost of implementation. The Trimble Nomad-Garmin GPS combination costs ~$2,100 U.S., which does not include the cost of the ESRI software license or desktop computer. However, as recent developments with GPS-enabled personal devices such as the Apple iPhone indicate, a combination of improved and cheaper technology, as well as free, customizable, open-source GIS software, is likely to substantially lower this cost in the near future.

The digital spot-mapping method is useful for scientific studies requiring accurate bird locations and may also be suitable for citizen science applications (Silvertown 2009). Many birding enthusiasts, just as they have long been equipped with binoculars and paper bird guides, now carry smart mobile phones with electronic bird guides from groups such as National Audubon Society. For example, the Apple iPhone application BirdsEye (http://ebird.org/content/ebird/news/BirdsEye) provides real-time access to the Cornell Laboratory of Ornithology's eBird data base, which contains millions of citizen-reported records showing where and when birds were observed in North America. The capacity to record information about birds with a digital spot-mapping application combined with a GPS, camera, and recorder to capture bird photographs and songs for later identification may enhance information gathering and minimize interpretation errors.

The potential of digital spot-mapping should improve as hand-held computing also improves. The mapping device of the near future will likely be a small, affordable, hand-held, touch-screen computer, equipped with a GPS unit capable of sub-meter accuracy, simple open-source GIS software loaded with (or accessing wirelessly) maps and high-resolution aerial photographs, and capability for syncing with a central storage server/computer for data transfer. The potential applications of such a device are myriad, and

digital mapping can be expected to revolutionize aspects of field ornithology.

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Variation of Type B Song in the Endangered Golden-Cheeked Warbler (*Dendroica chrysoparia*)

Wendy J. Leonard,[1] Jayne Neal,[1] and Rama Ratnam[2,3]

ABSTRACT.—The Golden-cheeked Warbler (*Dendroica chrysoparia*), a member of the Parulidae, uses a two-category song system referred to as Type A and Type B. However, songs recorded from adult males in Bexar County, Texas, USA, did not resemble the typical A or B songs reported for this species. We report an analysis of these atypical songs from six adult males. Quantitative features of the measured songs and syllable structure suggest this atypical song is more comparable to a B song than an A song with some modifications. The atypical song has dropped a terminal syllable of the known B song, and selectively modified one of the syllables to include frequency modulations (up and down slurs). Further, the known B song was not heard in the investigated sites. We conclude the atypical song is a variant of the B song. *Received 10 December 2009. Accepted 30 June 2010.*

The Golden-cheeked Warbler (*Dendroica chrysoparia*) (GCWA), a member of the Parulidae, has a two-category song system, referred to as ''first category'' and ''second category'' (Spector 1992). ''First category'' songs, used by unmated males during daylight, are used in disputes with other males and use declines after mating (Spector 1992). These songs, which can be simple and used near females, are usually sung at low rates (Bolsinger 2000). The ''second category'' song is used during the dawn chorus or before sunrise, and is more common later in the breeding season (Spector 1992). This song is more complex and faster than the first category song and is preceded with short call notes (chips) (Pulich 1976, Spector 1992, Bolsinger 2000). It can also be more variable than the first category song (Bolsinger 2000). Bolsinger (1997, 2000) uses the more common terminology 'A song' (for first category songs) and 'B song' (for second category songs).

One of the authors (JN) repeatedly heard a GCWA song in spring and summer of 2008 and 2009 that was not a typical A or B song. These birds were visually identified and confirmed to be GCWA. Males sang these songs throughout the season, although they were heard more frequently later in the breeding season. It was not evident whether the song was Type A or B. We recorded song sequences in 2009 from six individuals at three sites in northern Bexar County, Texas, USA. Our goal was to quantitatively compare the new song with reported songs for this species to correctly classify this song as an A or B song.

METHODS

Songs were recorded from adult male GCWAs on City of San Antonio, Texas properties. These sites included Grey Forest (29° 37′ 39″ N, 98° 42′ 4″ W), a City Park (29° 38′ 9″ N, 98° 38′ 24″ W), and a site near Camp Bullis (29° 37′ 12″ N, 98° 35′ 24″ W). We recorded over a distance of ~10 km in areas of deciduous woodlands and live oak/juniper (*Quercus/Juniperus*). Recordings were made using omnidirectional microphones (MKE-2, Sennheiser Electronic Corporation, Old Lyme, CT, USA) connected to a high resolution digital audio recorder (Model 722T, Sound Devices LLC, Reedsburg, WI, USA) that amplified and digitized signals at 44.1 kSamples/sec, and stored them as WAV files in the built-in hard drive. Songs were analyzed using Audition (Adobe Systems Inc., San Jose, CA, USA) and MATLAB (The MathWorks Inc., Natick, MA, USA). A band pass filter (sixth order, Type II Chebychev, 2.5 to 10.5 kHz) was used to eliminate energy outside the frequency band of GCWA songs. Spectrograms were generated for each segment using a Fast Fourier Transform (100-msec segments, Hann windowed, 95% overlap). Individual songs were extracted from the sequences by visually scanning the spectrograms.

Songs were divided into syllables, and each syllable was classified and given a lower-case letter designation. Quantitative analysis of songs followed Bolsinger (1997, 2000). Histograms

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TABLE 1. Components of known GCWA and atypical GCWA songs. Control data (A song, B song) are from recordings deposited at Macaulay Library. Atypical songs are from 6 males in northern Bexar County, Texas recorded in May and June 2009. Values in parentheses are ranges.

Song	Duration (sec)	Song complexity (elements/song)	Song rate (songs/min)	Pause duration (sec)	Number of chips preceding song	Frequency of modal intensity (Hz)
A song[1]	1.9[a] (1.6–1.9)	3[b]	5.1[a] (3.9–6.0)	10.2[a] (1.3–13.9)	0.7[a] (0–1)	5,354[a] (4,580–5,980)
B song[1]	2.0[a] (1.8–2.3)	5[b] (4–6)	6.8[a] (3.1–9.1)	8.1[a] (4.5–17.1)	5.1[a] (0–14)	4,863[a] (4,280–5,420)
Atypical song (2009)	2.1 (1.3–2.3)	5.8 (4–7)	5.8 (3.4–11.2)	9.0 (2.5–15.7)	3.5 (0–12)	4,675 (4,200–5,080)

[a] Data from recordings deposited at Macaulay Library, Cornell Laboratory of Ornithology. Audio record numbers: J. S. Bolsinger (A song birds = 4, B song birds = 3; circa 1994) 109301, 109338, 109340, 109734, 109736, 109749–109752, 109754, 109760, 109761; W. H. Gunn (B song bird = 1; c. 1977) 68956, G. A. Keller (A song bird = 1; circa 1986) 40560, 40561, T. A. Parker III (A song bird = 1; circa 1986) 38337, 38344, 38347, R. C. Stein (B song bird = 1; circa 1961) 9190–9195.

[b] Data from Bolsinger (1997:38, table 1.1).

were constructed for the following parameters: (1) song complexity (defined as the number of syllables per song), (2) number of chips preceding a song, (3) song duration, (4) pause duration (between songs in a bout), (5) song rate, and (6) frequency of modal intensity (defined as the frequency component with the greatest energy). Pause durations exceeding the 90th percentile were excluded from histograms as they indicated gaps between bouts. A and B song recordings made between 1961 and 1994 were obtained from the Macaulay Library (Table 1). The recordings served as control data and were analyzed similarly for number of chips, song duration, pause duration, song rate, and frequency of modal intensity. The frequency of modal intensity was measured from the spectrum of a syllable rather than the entire song (as adopted by Bolsinger 1997). The syllable was selected so it had comparable duration and frequency bandwidth across the set of atypical and control songs.

Statistical comparisons of parameters were performed among three groups: (1) the atypical 2009 recordings, (2) control A songs, and (3) control B songs. Song parameters were averaged over all songs for a given bird, and then averaged over the number of birds. Thus, sample sizes reflect the number of individual birds recorded, and not the total number of recorded songs. The goal was to ascertain if the atypical 2009 recordings were similar to the A song or the B song by comparing for differences in means of the measured parameters. All comparisons were performed using the Kruskal-Wallis test (Sokal and Rohlf 1995) to look for significant differences between means of the groups. A pair-wise multiple comparison test was used to examine which pairs of groups differed in their means. The multiple comparison procedures (with a Bonferroni correction) reported confidence intervals at α-level of 0.01.

RESULTS

Two hundred and fifty-nine songs were recorded from six adult GCWA males from 17 May to 13 June 2009. Numbers of songs produced by each bird (in decreasing order) were: 102, 63, 37, 26, 17, and 14. A total of 161 control A songs was obtained from recordings of six birds (numbers of songs were 67, 24, 21, 19, 16, 14), and 115 control B songs were obtained from recordings of five birds (numbers of songs were 35, 33, 19, 18, 10).

Representative control A and B songs (Fig. 1A, B, respectively) were compared with atypical songs (2 examples shown in Fig. 1C, D). A visual comparison of the spectrograms suggests the atypical song more closely resembles the known B song than the A song. However, there are differences in the number of syllables and the structure of the song. The known B song has five syllables labeled a through e (Fig. 1B) whereas the atypical song has only four syllables and lacks the terminal e syllable. Syllable a is markedly less intense in the atypical song and lacks the buzzy nature in the known B song. In some instances it was so faint as to be barely audible above the background noise. Syllable b is well-preserved and has been used to align the songs (Fig. 1B, C, D), and syllable d has been modified in duration but is otherwise unchanged. The greatest modification occurs in syllable c which in the known B song is a complex of two tonal elements centered between 6 and 4 kHz (Fig. 1B). This syllable (marked as c′ in Fig. 1C, D) in the atypical song has been lengthened and includes complex frequency modulations (up and down slurs); it is more variable across individuals than other syllables (Fig. 1C, D).

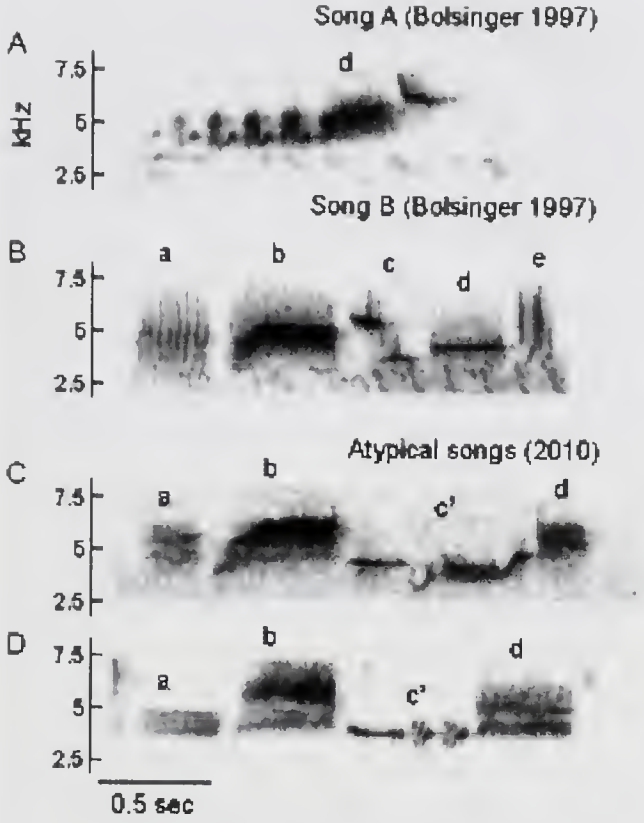

FIG. 1. Song spectrograms of (A) known A song, and (B) known B song. These songs were recorded between 1961 and 1994 and served as control data. C and D are atypical songs reported in this study. The known B and atypical songs are aligned on the offset of syllable b.

The similarities and differences between the known A, B, and atypical songs were quantified by analyzing song parameters (Table 1). Song complexity was similar for the atypical song and the known B song with the A song demonstrating less complexity. The A song is not normally preceded by chips and a comparison of the mean number of chips was possible only between the B song and the atypical song. Mean number of chips was significantly higher in the B song than the atypical song, but the number of chips produced had a similar range. Frequency of modal intensity was estimated from the d syllable for all songs. This syllable in the control A song was identified as the pre-terminal syllable (Fig. 1A) as it most closely resembles the d syllable in the atypical and control B songs. The mean frequency of modal intensity for the known B song (4,803 Hz) and atypical song (4,675 Hz) were closer to one another than to the A song (5,354 Hz), but they all significantly differed from one another, as did mean song durations for all pairs. There were no significant differences between song rates of the atypical and A or B songs, and the pause duration between the atypical and B songs. All other paired comparisons were significantly different.

DISCUSSION

The atypical GCWA songs recorded in 2009 in northern Bexar County are different from the B song reported for this species in a number of respects, but the spectrogram analysis, syllable similarity, and structure suggest this atypical song is likely to be a variation of the known B song (Fig. 1). Further, A songs are not usually preceded by chips or calls notes whereas the known B song and the atypical song were frequently preceded by chips. These findings suggest the atypical song is a B or "second category" song (Spector 1992) with a markedly modified c syllable, and lacking the terminal e syllable found in the control B song.

The typical A song was heard infrequently during the field investigations, but was not recorded. The atypical B song was heard more frequently during the later part of the GCWA breeding season. This agrees with the description of A and B song use by Spector (1992). A or "first category" songs dominate early in the breeding season and then decline after pairing (Spector 1992). B or "second category" songs are more common later in the breeding season (Spector 1992). We note the typical B song was not heard from these six birds during field investigations.

We propose the atypical song is the B song which has undergone variation over time. This has important implications for conservation. Accurate population estimates are essential for assessing the status of the federally listed endangered GCWA; these assessments often rely on auditory detections. Our study sites are in a region of Bexar County that is experiencing rapid urban development with clearing of oak and Ashe juniper (*Juniperus ashei*) woodlands necessary for breeding. Further investigations over several seasons are needed to identify the ecological significance and permanence of the song change. Are the changes in song structure temporary resulting from a loss of GCWA breeding habitat, a change in vegetation, or increased habitat fragmentation (Laiolo and Tella 2005)? Or, are the changes permanent resulting from changes in morphology (Derryberry 2009)? Our work is preliminary and was conducted late in the season. A more detailed study will be conducted next season to fully characterize this B song variant, but there is

sufficient evidence to warrant larger and detailed surveys of the species over its breeding range, particularly in isolated and fragmented habitats.

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Nocturnal Social Cues Attract Migrating Yellow-breasted Chats

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ABSTRACT.—We tested the hypothesis that migrating birds use nocturnal conspecific song when selecting stopover habitat using data from the Yellow-breasted Chat (*Icteria virens*). We broadcast nocturnal song in unsuitable habitat (i.e., a manicured orchard) and alternated broadcast nights with nights where no song was broadcast. We caught significantly more individuals (8 males, 7 females) on mornings following treatments relative to control nights when no songs were broadcast (2.5 vs. 0 birds/morning, respectively). Eleven of 15 (73%) chats were removed from the nets after sunrise (mean = 32 min after sunrise, range = 5–60 min), and birds were captured on overcast, cloudy, and clear mornings. Only one bird was recaptured at the site, and only one male was detected singing at the site, suggesting individuals quickly left the area. Conspecific nocturnal songs for chats appear to be an important cue for selecting stopover habitat. *Received 8 March 2010. Accepted 9 July 2010.*

Reliable cues of high-quality habitat are important for migratory birds because energetic and fitness costs of not locating suitable habitat are likely high. Migratory birds use a suite of navigational cues to migrate between wintering and breeding areas (Able and Bingman 1987); however, the specific cues used to select stopover habitat remain largely unknown. Studies suggest that both visual (Moore et al. 1995) and acoustic cues (Ward and Schlossberg 2004, Mukhin et al. 2008) may be involved. However, many nocturnally migrating passerines select stopover locations prior to sunrise (Cochran et al. 1967, Moore and Aborn 2000) when visual cues may be absent or difficult to evaluate. Cues that facilitate locating suitable habitat are likely highly valuable for migrating birds, and one may be nocturnal song.

Nocturnal song by diurnally active birds appears to be uncommon; however, recent research suggests nocturnal song may be an important habitat location cue (Herremans 1990, Schaub et al. 1999, Mukhin et al. 2008). Several diurnally active species that sing at night have specific nocturnal songs. For example, research on Common Nightingales (*Luscinia megarhynchos*) suggests males sing a whistle song at night to attract females (Glutz von Blotzheim 1988, Amrhein et al. 2002, Roth et al. 2009). The

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nocturnal song of Yellow-breasted Chats (*Icteria virens*) is also given at a frequency and amplitude that may allow detection farther than their diurnal song (Canterbury 2007). Female and male chats may use this song as an indicator of suitable habitat and mates. However, the relative importance of conspecific vocalization versus habitat cues is unknown.

We broadcast the nocturnal song of male Yellow-breasted Chats, a song that is consistently sung at night during spring migration (Canterbury 2007), in unsuitable habitat during spring migration. The shrubland habitat in which chats stopover is patchy, and the probability of a migrating individual quickly locating suitable habitat at dawn is unlikely; thus, birds would benefit by using pre-dawn cues to locate appropriate areas. We hypothesized that both male and female chats use nocturnal song as an indicator of suitable habitat, and that both males and females would select areas with conspecific nocturnal song regardless of habitat suitability. We predicted that chats attracted to unsuitable habitat would quickly leave the site once they found it was unsuitable.

METHODS

This experiment was conducted on University of Illinois property in southeast Urbana, Champaign County, Illinois, USA during spring migration between 29 April and 15 May 2009. The site was a 210 × 30 m linear strip of six rows of apple (*Malus* spp.) trees spaced 6.5-m apart with mowed strips of grass between each row of trees. The habitat north and east of the site was residential and commercial property, while the habitat to the west and south was a mixture of agricultural land with additional patches of apple trees and mature forest. The area was selected because it offers woody vegetation, but lacked the size and dense shrub layer that chats require for both breeding (Thompson and Nolan 1973) and stopover habitat (Parnell 1969). Yellow-breasted Chats are not known to nest within the Champaign city limits (Kleen et al. 2004), and the nearest shrubland with breeding chats is ~16 km away. The site is routinely monitored during statewide bird surveys and other research projects, and chats have yet to be recorded at this location.

We alternated between control nights, when no songs were broadcast, and treatment nights with song playbacks when the weather allowed (i.e., not raining). We used a mixture of commercially available chat songs (Elliott et al. 2000) and chat songs we recorded from individuals in east-central Illinois. The recording included a male whistle song, the song only used at night (Canterbury 2007). The entire recording was 100 sec in length and was repeated continuously using a Fox Pro FX3 playback system. The whistle song was imbedded in two locations during the 100-sec playback: 15 sec and 80 sec, and was 0.5 sec in duration. We placed the system in the center of the site in a weatherproof plastic container and directed the device at a 45° angle southward toward the sky. Songs were broadcast on treatment nights from sunset to 1.5 hrs after sunrise. We placed mist nets approximately every 30 m on the site to increase the probability of capturing all chats moving through the vegetation; nets were numbered 1 (South net) to 6 (North net) and were opened for 1.5 hrs before and after sunrise each morning for both treatment and control nights. Nets were checked every 20 min for birds. We banded all captured chats with a USGS band, recorded gender, and the net number in which each individual was captured prior to releasing them at the site. We conducted 5-min, unlimited-radius point counts each morning in two locations at the site after closing the nets to quantify the number of singing chats. One point was at the southernmost end of the strip while the other was at the northernmost end. We conducted a Chi-square test to examine if chats were captured more often than expected on mornings following treatments.

RESULTS

We captured 15 chats (8 males, 7 females) during four of six mornings that we broadcast chat song at night and captured no new individuals during any of the five control mornings (χ^2 = 12.5, $P < 0.001$). Eight of 15 chats (53%) were captured in nets closest to the speaker (chat song), while seven (47%) were captured in the southernmost nets. Eleven of 15 (73%) chats were removed from the nets after sunrise (mean = 32 min, range = 5–60 min), and birds were captured on overcast, cloudy, and clear mornings. Only one male chat was heard singing during point counts and it was during the morning he was captured. No male chats were recorded singing on control days. Only one individual was recaptured; a female 3 days after initial capture.

DISCUSSION

Migrating chats were captured only on mornings following nights when conspecific vocalizations were broadcast; no birds were captured during mornings following nights with no song. Both migrating male and female chats responded to experimental addition of nocturnal male song, suggesting male chat song functions as a cue for selection of stopover habitat. Male chats did not establish territories and vacated the area. The lack of appropriate habitat did not preclude chats from briefly stopping, as long as conspecific songs were present.

Nocturnal song of diurnally active birds has been documented, primarily in species that breed in patchy or ephemeral habitat (Barclay et al. 1985, Walk et al. 2000). For example, male Common Nightingales breed in ephemeral habitat (Hewson et al. 2005) and also sing nocturnally for mate attraction (Amrhein et al. 2002). Male chats also appear to primarily use long-range whistle songs only at night (Canterbury 2007). Male chats will sing continuously at night for up to 6 days after arrival in breeding areas, potentially providing abundant social cues early in the season when most females are returning from wintering locations (Canterbury 2007).

We broadcast nocturnal song between sunset and 1.5 hrs after sunrise, and chats were attracted either during the night or shortly after sunrise. Selecting stopover habitats at sunrise may be adaptive if increased visibility allows for better habitat assessment (Bolshakov and Bulyuk 1999); these results suggest that, at least for chats, individuals are selecting habitat based on social cues. Visibility can also have a role in affecting the importance of social cues (Herremans 1990); birds in our study were captured during cloudy, overcast, and clear mornings, but whether visibility had a role in why birds were captured is unknown.

Conspecific attraction has received increasing attention in recent years, and is important for both habitat selection and planning conservation and management actions (Ahlering and Faaborg 2006). Several studies have demonstrated that birds use conspecific attraction to assess and select habitat (Mukhin 2004, Serrano et al. 2004, Ward and Schlossberg 2004, Ahlering 2005, Betts et al. 2008, Ktitorov et al. 2010). Most conspecific attraction studies have not attempted to attract birds to unsuitable habitat, nor have studies focused exclusively on nocturnal song (but see Mukhin et al. 2008, Ktitorov et al. 2010). Attracting birds to unsuitable rather than suitable habitat is a more reliable method of assessing the importance of acoustic social cues (Chernetsov 2006, Betts et al. 2008).

Heterospecifics may also use these cues while selecting habitat (Mönkkönen et al. 1999). We did capture other shrubland bird species on mornings following treatments, including Orchard Orioles (*Icterus spurius*), Brown Thrashers (*Toxostoma rufum*), and Field Sparrows (*Spizella pusilla*), but either did not capture or caught fewer individuals following control nights. These species do not commonly breed in developed areas. A separate playback experiment is necessary to examine if these species use chat song in addition to vegetation structure to select suitable habitat. Many of the bird species that breed in patchily distributed habitats in North America are known to sing at night (Barclay et al. 1985, Walk et al. 2000) and may be using nocturnal heterospecific song as a cue during migration; future research is needed to address conspecific and heterospecific attraction in shrubland birds.

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Range Expansion of the White-breasted Waterhen (*Amaurornis phoenicurus*) into Micronesia

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ABSTRACT.—We report the first occurrence of the White-breasted Waterhen (*Amaurornis phoenicurus*) in Oceania based on discovery of a breeding population on Woleai Atoll, Yap, Micronesia. Islanders believe it first arrived on Woleai in the early 1970s, at a time when the species was beginning a period of range expansion that may be ongoing. Yap Outer Islanders report the waterhen is present also on nearby Eauripik, Ifaluk, and Faraulep atolls, where it arrived after it colonized Woleai. We summarize extralimital, nonbreeding dispersal of *A. phoenicurus* and report a recent first record for Palau. *Received 15 January 2010. Accepted 28 April 2010.*

The White-breasted Waterhen, *Amaurornis phoenicurus* is known to breed from Pakistan, India, Sri Lanka, and the Maldive Islands east through southeast Asia to Japan and the Philippines, and south to Christmas and Cocos (Keeling) islands (Australian Indian Ocean Territory), and the Lesser Sundas (Taylor 1996). Steadman (2006) reported that it is not indigenous to tropical Oceania now or prehistorically, and makes no mention of any vagrant sightings of it. We report the first known occurrence of this species in Oceania based upon a breeding population on Woleai Atoll, Yap, Micronesia, hitherto known only to island residents.

LOCALITY

Woleai Atoll (07° 23′ N, 143° 55′ E) is within Yap State, one of four states (along with Chuuk, Pohnpei, and Kosrae) comprising the Federated States of Micronesia (FSM) (Fig. 1). The FSM and the Republic of Palau, immediately to the west, are in the Caroline Islands, which span ~3,000 km of the west-central Pacific Ocean between the Philippines and Indonesia to the west and the Marshall Islands to the east. Woleai Atoll comprises 22 low (4 m maximum elevation asl) coralline islands distributed along a barrier reef around a 23.4 km^2 lagoon. The total land area is ~4.5 km^2; Falalop is the largest island (1.53 km^2). The nearest land area is Ifaluk Atoll, 50 km to the east, Eauripik Atoll is 115 km to the southwest, and Faraulep (= Feshaiulep) Atoll is 150 km to the northeast. Sorol Atoll and the high islands of Yap proper are ~390 and 660 km to the northwest, respectively. The vegetation on Falalop, Woleai, consists largely of coconut (*Cocos nucifera*) agroforest, secondary woodland (shrubs and small trees), and marsh vegetation in swampy areas where people often cultivate taro (*Cyrtosperma chamissonis*). Archaeological data for Woleai are lacking, but the earliest known dates of occupation for Fais Island and Ngulu, Ulithi, and Lamotrek atolls among Yap Outer islands range from 1,200–1,900 BP (Intoh 1997, Rainbird 2004). The national census in 2000 recorded 975 residents on Woleai (Yap Branch Statistics Office 2002).

OBSERVATIONS

On 18 June 2009, while collecting insects on Falalop Island, Woleai Atoll, DWB heard several *A. phoenicurus* calling at different locations in low, wet areas along the airstrip and in the vicinity of the settlement. He saw none of the birds during ~6 hrs on the island, and identified the calls in retrospect. He queried several local residents and learned only that the bird was called Kuwakuwa, an onomatopoeic rendering of its call, and that it probably arrived on the island about 30 years ago. The residents' descriptions of the bird were surprisingly vague, considering its distinctive appearance.

In response to our request to teachers on Woleai for a photograph or a specimen, Ellisa Siyaneral and Julian Yangerely captured a bird, which died shortly thereafter, in mid-July 2009. The specimen was frozen and subsequently delivered to SR on 19 August via the government field trip ship. Eddie Haleyalig delivered photographs of the

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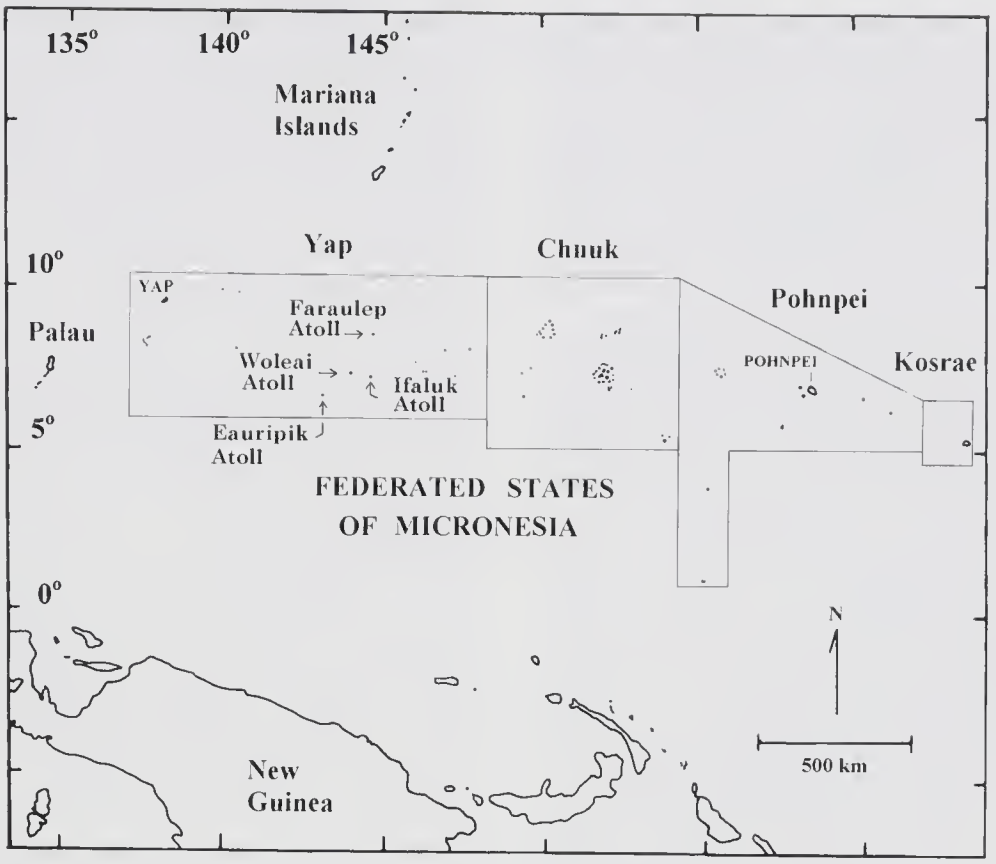

FIG. 1. The Federated States of Micronesia and islands where *Amaurornis phoenicurus* has been reported.

specimen, taken by his daughter Jennifer, to DWB, who identified it as *A. phoenicurus*. DWB prepared the bird as a study skin and deposited it in the collection of the Natural History Museum, Tring, UK (BMNH # 2010.13.1).

We distributed a questionnaire among Woleai residents, and 22 of 30 respondents reported seeing nests of the Kuwakuwa, 20 of 20 indicated nests were in or near taro patches, 23 of 31 reported seeing eggs of this species, and 21 of 26 observed young, all on Falalop Island. Angelburt Igemera, a student at College of Micronesia, reported having seen a nest with eggs on Seliap Island, and student Dickson Tiwelfil reported hearing and observing the Kuwakuwa in taro patches on Wottegai Island. These and other responses indicate the White-breasted Waterhen is present on all of the inhabited islands of Woleai Atoll. We are confident these reports all pertain to *A. phoenicurus* as there are no other rallids on the atoll and no other species with which it is likely to be confused.

The extent of this species' distribution elsewhere among the Yap Outer Islands is uncertain. Interviews with islanders indicate this species is present at least on Eauripik, Ifaluk, and Faraulep atolls, and that it probably arrived on these islands from Woleai. Julius Sapelalut (pers. comm.), Chief Public Defender, FSM Public Defenders Office, and former resident of Ifaluk, reported that *A. phoenicurus* was not seen on Ifaluk until the early-to-mid-1980s, by which time it was already well established on Woleai. Breeding has not been confirmed on Ifaluk, but is probable because the birds are heard calling year-round (J. Sapelalut, pers. comm.). John Haglelgam (pers. comm.), a professor at COM, reported his sister recalled flushing a Kuwakuwa from a nest containing one egg in a taro patch on Eauripik Atoll in 2008, and Mickael Rapiy (pers. comm.) reported encountering this species on Faraulep Atoll a number of years ago, after first having seen it on Woleai ~2 years earlier. The distribution and abundance of *A. phoenicurus* in central Yap State atolls requires further study to supplement these anecdotal accounts.

Additionally, Mark Vereen, a resident of Ngermetengel, on the west side of Babeldaob Island, Palau, observed a White-breasted Waterhen in his yard daily from 30 October to 3 November 2009. The bird was initially identified by Doug Pratt from photographs taken by M. Vereen, documenting the first record of *A. phoenicurus* for the Republic of Palau. It was

usually seen at the edge of dense vegetation, and not far from an extensive wetland area. It often mingled with domestic chickens and was occasionally observed feeding on earthworms in a perpetually wet area of the yard. The disappearance of the bird was coincidental with the acquisition of two young dogs that roamed the yard freely.

RANGE EXPANSION AND DISPERSAL

The appearance of the White-breasted Waterhen in Micronesia apparently is coincident with a broad range expansion by this species. *Amaurornis phoenicurus* is resident year-round throughout most of its breeding range, but northern birds are migratory and winter as far south as Sumatra, and as far west as the Arabian Peninsula (Taylor 1996). Quantitative data on migration and dispersal are largely lacking, but Desmond Allen and P. D. Round (correspondence, April 2010) recorded 106 trapped during banding surveys at Dalton Pass, Luzon Island, Philippines, during November and December 2009. It was the most numerous of 12 species of rallids encountered during the survey. To what extent these were birds originating from outside the Philippines, is unknown.

The waterhen was rarely seen in Japan until the 1970s, but was then observed with increasing frequency, and first recorded breeding in Kyushu in 1982 (Nakamura 1987). It is now a year-round resident in Japan's Ryukyu Islands and Haha-jima in the Ogasawara (= Bonin) Islands and continues to advance northward into the Japanese main islands (Brazil 1991, Taylor 1996). The waterhen is now so common on Iriomote Island that it may be displacing the Slaty-legged Crake (*Rallina eurizonoides*) there (Taylor 1996). Sakaguchi and Ishihira (1998) attributed an increase in the number encountered on Iriomote Island during March-May to an influx of breeding adults, and Nakamura (1987) indicated ~73% of the birds recorded in Japan were from March to August with the highest frequency in May.

The White-breasted Waterhen was first recorded in Korea in 1970 and a failed breeding attempt was recorded there in 2001 (Park 2002, Moores 2007). The first recorded successful nesting in Korea was in 2008 and two young were observed at Namyang Bay on 30 August (Edelsten et al. 2008). The waterhen was first recorded on Seram in the Moluccas in 1987 (Bowler and Taylor 1989), and may now be resident there (Coates and Bishop 1997). Colonization of Australian Indian Ocean Territory islands may have been at approximately the same time. Two young produced by a breeding pair in 1993, and again in 1994, and incidental sightings of other adults were the first records of *A. phoenicurus* on Christmas Island (Carter 1994), and the waterhen probably became established as a resident breeder on Cocos (Keeling) Islands sometime between the late 1990s and 2004 (Johnstone and Darnell 2004, Dooley 2005, Reid and Hill 2005, Hadden 2006). The White-breasted Waterhen was first recorded on the Arabian Peninsula in Oman in 1977 (Gallagher and Rogers 1980), and Pedersen (2008) considered it a rare to uncommon winter visitor in Dubai (United Arab Emirates). One photographed on 30 October 2009 is the first record for Saudi Arabia and the northernmost record for the Arabian Peninsula (Lobley and Roberts 2010), but the birds have not yet bred anywhere on the peninsula (M. C. Jennings, pers. comm.).

Examples of long distance dispersal or vagrancy in this species include: one found alive in the Seychelles on 24 December 1991 (Skerrett 1994); one found dead in central Mongolia and another in southern Mongolia in May 2004 and June 2004, respectively (Gombobaatar et al. 2005); several records from the Russian Far East, including one found dead on Bolshoy Pelis Island on 20 June and another in the Olginskiy District on 15 July 1987 (Nazarov and Kazykhanova 1988); one observed in the Sikhote-Alin Nature Reserve on the Pacific Coast of Sikhote Mountains in 1996 (Elsukov 1999) and another on Sakahlin Island on 20 September 1994 (Kozin 1995); one was captured, banded, and released on the Avacha River near Elizovo, northwest from Petropavlosk-Kamchatskiy, Kamchatka Peninsula on 1 November 1996 (Gerasimov 1996).

DISCUSSION

We do not know exactly when White-breasted Waterhens first arrived on and colonized Woleai Atoll. The consensus among islanders we interviewed suggests the species became established in the early 1970s, which would roughly coincide with the early stages of this species' ongoing range expansion. None of the elders we interviewed recalled seeing it any earlier, and none was recorded anywhere in Micronesia by Baker (1951), who included records of other species encountered on Woleai by Japanese ornithologists

during the early 1900s. That a resident population has gone unreported from Woleai for over 30 years is readily explained by the absence of knowledgeable observers. Commercial flights to the atoll have been, and continue to be, infrequent and irregular. The FSM and Yap State government ships also visit Woleai irregularly, but usually spend only a brief part of a day before continuing on.

Comparisons of photographs of the bird from Woleai with specimens at the American Museum of Natural History by Mary LeCroy, and at the Smithsonian Institution by Storrs Olson, indicate the Woleai specimen is within the range of variation of the nominate subspecies. The other subspecies tend to have either less (*A. p. leucomelanus*, Sulawesi, Moluccas, and Lesser Sundas) or more (*A. p. insularis* and *A. p. midnicobaricus*, Andaman and Nicobar Islands) white in the forehead (Taylor (1996). The bird photographed at Palau also appears to be an example of the nominate subspecies (photographs examined by DWB and Doug Pratt). The waterhen population on Woleai could have originated from the nearest sedentary population of *A. p. phoenicurus* in the Philippines, but more likely from migratory northeast Asian birds that strayed east from their usual migratory path. The White-breasted Waterhen appears to have bypassed Palau, Yap, and the Marianas, high islands with seemingly suitable habitat much nearer to potential source populations, in establishing a foothold in Micronesia. The waterhen's furtive and skulking habits may limit sightings, but its loud and frequent vocalizations make it hard to overlook. Possibly the recent Palau sighting is a harbinger of wider colonization of Micronesia.

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First Reproductive Record of Wilson's Plover in Baía de Todos os Santos, Northeastern Brazil

Vitor O. Lunardi[1,3,4] and Regina H. Macedo[2]

ABSTRACT.—The Wilson's Plover (*Charadrius wilsonia*) is widely distributed along the coast of the Americas. We present the first reproductive record in Baía de Todos os Santos, Brazil, broadening the southernmost limit of its breeding area along the Atlantic Coast to 12° 44′ S, 38° 45′ W. We recorded a family with a subadult in 2007, and a family with chicks and a nest in 2008. The female invested more time in incubation than the male in 96 hrs of diurnal nest observations. There were 102 interruptions during incubation due to the approximation of domestic animals (cattle and horses). The nest was abandoned 9 days after egg laying. An experiment with artificial nests suggests that 30% of Wilson's Plover nests may be destroyed by free-ranging domestic animals in this Baía. *Received 11 January 2010. Accepted 5 June 2010.*

The Wilson's Plover (*Charadrius wilsonia*) is a widely distributed Charadriidae associated with coastal habitats in the Americas with resident populations in numerous sites. It breeds on the Atlantic Coast, between the eastern USA and northeastern Brazil, in the Caribbean Islands, and on the Pacific Coast, between Mexico and northwestern Peru (Corbat and Bergstrom 2000). The species exhibits plumage differences throughout its range, which attracted the attention of systematists, leading to subdivision of the species into five subspecies (Wiersma 1996, Corbat and Bergstrom 2000, Grantsau and Lima 2008). Wilson's Plover is seemingly monogamous (Corbat and Bergstrom 2000), and both males and

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females are capable of performing incubation (Bergstrom 1981).

Historically, the breeding range of Wilson's Plover has been contracting and reproductive populations in the current northernmost limit are threatened, mainly due to destruction of breeding areas and interference during reproduction and while resting. However, little is known about threats outside this region (Corbat and Bergstrom 2000).

Records of reproduction and information about populations of Wilson's Plover in the Southern Hemisphere are scarce and restricted to a few sites (Tovar 1968, Rodrigues et al. 1996, Wiersma 1996, Corbat and Bergstrom 2000, Grantsau and Lima 2008). We describe: (1) the first breeding record of Wilson's Plover in the southernmost limit of its breeding range on the Atlantic Coast (Baía de Todos os Santos, Brazil), and (2) features of the species' reproductive behavior and potential threats to the study population.

METHODS

Monitoring of Nests and Families.—We recorded breeding of Wilson's Plover in the coastal region of Saubara, Bahia, western coast of Baía de Todos os Santos, Brazil (12° 44′ S, 38° 45′ W). This region is characterized by a complex of salt marshes (restingas), mangroves (*Rhizophora*, *Laguncularia*, *Avicennia*), supratidal salt flats (apicum), and intertidal areas. The climate is humid tropical with distinct dry (Sep–Feb) and rainy (Mar–Aug) seasons. We compared photos of individuals from the study site for species identification with specimens deposited in the Museu de Zoologia da Universidade de São Paulo–MZUSP (specimens: 41395, 41396, 42745, 80034, and 80035). We based our comparisons on the Wilson's Plover subspecies identification key to the Atlantic Coast developed by R. Grantsau (Grantsau and Lima 2008).

OBSERVATIONS

The first evidence of breeding of Wilson's Plover in the region was the record of a family, comprising a pair with a subadult, foraging in the intertidal zone on 17 December 2007. The following year, we found a Wilson's Plover nest with two eggs on 13 August 2008 in a restinga area. The next morning, taking advantage of the absence of the pair from the nest, we took nest and egg measurements and recorded a third egg

FIG. 1. Nest and chick of Wilson's Plover at Baía de Todos os Santos, Brazil. Photographs by Vitor O. Lunardi.

(Fig. 1). We performed 96 hrs of focal observation of the nest to examine parental investment in incubation, between 0600 and 1800 hrs, during the first 8 days of incubation (14 to 21 Aug 2008). Observations were conducted from a fixed point inside of the mangrove, 26 m from the nest, to avoid investigator disturbance. The nest with the eggs was abandoned on 22 August 2008, probably due to the intense disturbance by domestic animals (cattle and horses). The nest with eggs remained intact until 30 August 2008, when they were found destroyed.

On 27 August 2008 we found another family of Wilson's Plover with three chicks in an apicum area. Each chick (Fig. 1) was measured, weighed, and marked with a metal band (CEMAVE/Brazil). This family remained for the next 7 days at the

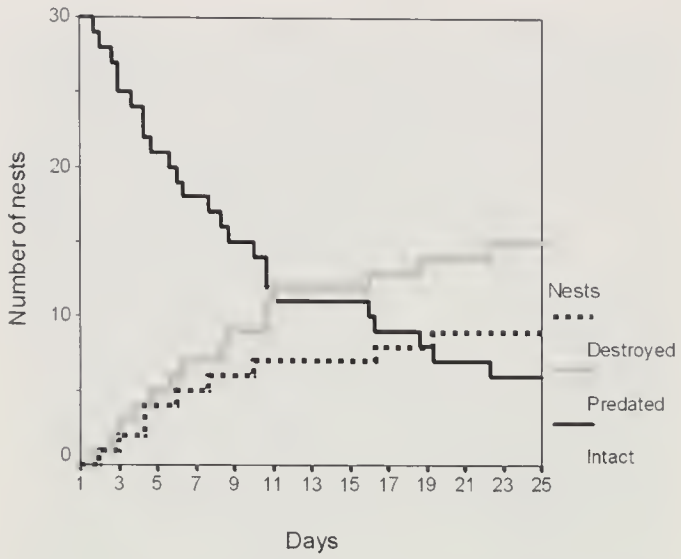

FIG. 2. Number of artificial nests destroyed, predated, and intact in a restinga area at Baía de Todos os Santos, Brazil, during 25 days.

same site with the aggregated chicks always accompanied by the adults.

Experiment to Verify Predation Intensity.—We observed Wilson's Plover pairs defending territories in a restinga area between May and October 2007 and 2008, also used as pasture by free-ranging cattle and horses from the local community. We conducted an experiment with artificial nests to estimate nest loss considering these animals may destroy nests. We built 30 artificial nests (cavities in the soil similar in shape and size to Wilson's Plover nests) in January 2009, placed in a series, 30 m apart, along a strip of restinga. We added three Common Quail (*Coturnix coturnix*) eggs to each artificial nest. We made three daily visits to each nest (0600, 1200, and 1800 hrs) over 25 days (approximate incubation time for the species) to record nests that were: (1) intact, (2) destroyed (with at least 1 destroyed egg and tracks of domestic animals), and (3) predated (absence or destruction of at least 1 egg; no signs of domestic animals).

Nine of 30 artificial nests (Fig. 2) were destroyed with 77.7% of occurrences during the day (0600–1800 hrs). Fifteen nests were predated with 66.7% of these events at night (1800–0600 hrs).

Monitoring of Nests and Families.—The only nest found consisted of a 25-mm cavity in sandy soil with a diameter of 102 mm and fragments of dry vegetation around the eggs. It was next to horse feces and a shrubby false buttonweed (*Spermacoce verticillata* L., Rubiaceae; height 17.5 cm) surrounded by grasses (Fig. 1). The three eggs measured: length = 34.9, 34.8, and 34.2 mm; width = 25.2, 25.0, and 24.4 mm; and mass = 14.0, 14.0, and 13.5 g. The eggshells were colored light cream with dark brown stains over the entire surface, but with a higher concentration on the blunt end.

The female invested 53.3 hrs (93.3%) in incubation during the observation period while the male invested 3.8 hrs (6.7%). The female was observed incubating between 0600 and 1733 hrs, and the male after 1714 hrs. The female interrupted incubation 125 times ($\bar{x} \pm$ SD = 1.29 ± 1.41/hr, n = 96) of which 102 (81.6%) were caused by approach of domestic animals, mainly cattle. After leaving the nest, the female often exhibited alarm and distraction behaviors: *squatting*, *head-up* (followed by vocalization), *mock-brooding* and/or *broken-wing*. In 54.3% of these interruptions the male approached the nest, exhibiting *head-up* and *crouch-run* display (behavioral descriptions in Bergstrom 1988b). The female was reluctant to return to the nest after disturbances.

The measures obtained for the three chicks were: right tarsus = 23.5, 23.3, and 22.1 mm; culmen = 17.3, 16.8, and 16.1 mm; and mass = 17.0, 16.5, and 15.5 g. The beaks were black; legs and feet grayish; plumage upperparts were brownish and black in a scalloped pattern, and underparts and neck were white. The age and gender of the chicks could not be assigned.

DISCUSSION

We present the first breeding record of Wilson's Plover in Baía de Todos os Santos, Brazil. This is the southernmost record on the Atlantic Coast for the species, representing an extension of their breeding range (Corbat and Bergstrom 2000, Grantsau and Lima 2008). Grantsau and Lima (2008) recorded breeding for Wilson's Plover (*C. wilsonia brasiliensis*) in Mangue Seco, Brazil, ~230 km north of Baía de Todos os Santos. The plumage of the males and females in our study area was similar to that of *C. w. brasiliensis* deposited at MZUSP, and suggests our records correspond to this subspecies.

Bergstrom (1988a) reported Wilson's Plover nests mainly near vegetation and occasionally near objects (e.g., cow manure, stones), emphasizing that both may function as a protection barrier against the wind. Objects and vegetation provided protection for the nest that we found against

easterly and southeasterly winds, which are predominant in August, when we found the nest.

The number, dimensions, and color of the eggs and size of the chicks we report are similar to those previously published for the species (Rodrigues et al. 1996, Corbat and Bergstrom 2000, Grantsau and Lima 2008). The female invested more time in diurnal incubation than the male. However, the male may have invested in nocturnal incubation, since they initiated this activity at the end of the day. Previous observations for the species indicate males incubate mainly at night (Thibault and McNeil 1995).

The experiment with artificial nests revealed that, in addition to natural threats (predators), use of coastal areas for grazing is another hazard to the reproductive success of Wilson's Plover in Baía de Todos os Santos. Trampling by roaming animals was previously considered a potential threat for Wilson's Plover eggs and recent hatched nestlings at Ilha do Curupu, Maranhão, Brazil (Rodrigues et al. 1996). Plovers leave their nests when disturbed and are extremely reluctant to return when intruders are present near nest sites. The constant interruption of incubation by interference may lead to inadequate egg temperature regulation, and exposing eggs to predation and overheating (Corbat and Bergstrom 2000). The female often left its nest when disturbed by free-ranging cattle and horses. Both females and males invested actively in predator avoidance behaviors. We assume the intense disturbance was the primary cause of nest and egg desertion.

Our observations confirm Baía de Todos os Santos as a breeding area of Wilson's Plover, extending the limit of its breeding range. Use of coastal areas for grazing is critical to consider in any project directed at conserving this population.

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Hatching Synchrony, Green Branch Collecting, and Prey Use by Nesting Harpy Eagles (*Harpia harpyja*)

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ABSTRACT.—We observed an occupied Harpy Eagle (*Harpia harpyja*) nest over three separate periods in eastern Venezuela. Both eggs in the clutch hatched on the same day, and two nestlings competed in the nest for 14 days before one succumbed. The female adult collected green branches 45 times over 60 days of observation. Green branch deliveries were positively associated with prey deliveries and our observations best support the 'nest sanitation by covering prey' hypothesis for the adaptive significance of green branch collecting. Prey delivery rate to the nest averaged one delivery every 2.4, 2.1, and 3.7 days in the three observation periods. Three-toed sloths (*Bradypus tridactylus*) and wedge-capped capuchins (*Cebus olivaceus*) were the most common prey items brought to the nest. *Received 14 April 2010. Accepted 23 July 2010.*

The Harpy Eagle (*Harpia harpyja*) is one of the largest and most emblematic eagles in the world, and is a species of considerable conservation concern throughout its range in Central and South America (Vargas et al. 2006). However, remarkably little is known of its ecology and behavior. The main reasons for this lack of knowledge are that Harpy Eagles are hard to locate and observe in the rainforest habitats in which they live. Much of what is known about their behavior comes from observations during nesting and chick rearing when their movements become centered on a nest (summarized by Schulenberg 2009). However, because of the difficulty in observing nests (they are usually positioned 20 m or more up in the canopy), only a few studies have been made and behavior at the nest is still poorly understood. For example, Harpy Eagles have been observed to collect green branches (i.e., branches with green foliage) during the nesting period (Rettig 1978), a behavior seen in many species of raptors. The adaptive signifance of this behavior remains unknown. Several hypotheses have been put forward including: (1) nest sanitation by repelling insects with the volatile components of leaf chemistry, (2) nest sanitation by covering prey remains, (3) advertisement of nest occupancy, (4) maintenance of humidity in the nest, and (5) provision of shade for the nestlings (Wimberger 1984).

Little is known about factors affecting prey use by Harpy Eagles during nesting, and only limited data are available (summarized by Schulenberg 2009). Harpy Eagles are distributed over a large geographic area, and the composition of prey species varies considerably in different parts of its range (Emmons and Feer 1997). It is probable that regional variations in relative abundance and ease of catching prey also occur.

Our objectives were to: (1) use quantitative and qualitative observations of Harpy Eagle nesting behavior to explore the adaptive significance of green branch collecting, (2) report prey use by a pair of nesting Harpy Eagles in a fragmented forest habitat in Venezuela, and (3) report an unusual case of hatching synchrony and extended sibling competition.

OBSERVATIONS

We observed an active Harpy Eagle nest for 60 days over three separate periods (2 May–2 Jun 2009, 5 Aug–3 Sep 2009, 8 Jan–10 Feb 2010) in the Sierra Imataca of Bolivar State, eastern Venezuela (07° 56.926′ N, 61° 43.244′ W). We monitored the nest from a blind on an arboreal platform 25 m from the ground ~60 m from the nest tree, a tall (>35 m) silk-cotton or ceiba tree (*Ceiba pentandra*). The nest was also monitored using a small remote camera fixed to a branch ~3 m above the nest platform.

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Green Branch Collecting.—Harpy Eagles collected branches with green leaves on 46 separate occasions in the 60 days the nest was observed. The female collected the green branches in all but one occasion. Most often the female would arrange the green branches over prey remains. She did not cover the chick(s) with green branches and hypothesis # 5 is not supported by our observations. The ambient humidity of the rainforest habitat is high, suggesting that hypothesis # 4 is unlikely to explain the main function of green branches in the nest. One or more green branch deliveries appeared more likely to occur on days when prey was also delivered, but this association was not statistically significant (2×2 contingency table: $\chi^2 = 2.39$, df = 1, $P = 0.12$). However, there was a period of 3 consecutive days during an exceptionally long fasting period when the female's green branch collecting behavior was atypical in that (1) it was much more frequent than usual (branch collecting observed 13 times in 3 days compared to the expected frequency of 5.7 based on the average green branch delivery rate on 'normal' delivery days), and (2) the female jettisoned 38% of these green branches before reaching the nest, which was not normally done. If these 3 days of unusual behavior are omitted from the statistical analysis, the association between green branch collecting and prey delivery becomes significant (2×2 contingency table: $\chi^2 = 3.94$, df = 1, $P < 0.047$). These observations support hypothesis # 2. We observed flies and other winged insects frequently flying around the nest. The female and the remaining chick responded to flying insects by vigorously shaking their heads or snapping with their beaks. The female or chick would react in this way to flying insects at least once on 9 of the 21 observation days (i.e., 43% of days) in the first observation period (chick 0–21 days of age). This contrasts with the second observation period (chick 95–112 days of age) when they reacted to flying insects only once in 15 observation days (i.e., 7% of days). We saw the female peck at crawling insects in the nest at least once in 10 of the 21 observation days (i.e., 48% of days) during the first observation period, while in the second period, we observed this behavior on only 3 of 15 observation days (20% of days). Responses to arthropods and green branch collecting were more frequent in the first period when the chick was more vulnerable (average 1.3 branch deliveries/day in the first period vs. 0.9 deliveries/day in the second observation period). These observations support both (#'s 1 and 2) nest sanitation hypotheses for green branch collection by Harpy Eagles. Most of the green branches were from the *C. peutaudra* tree which supported the nest, but some were also taken from a nearby fig (*Ficus* spp.) tree. Branches were taken from another tree species on only one occasion.

Prey Delivery.—We recorded 23 prey deliveries in the 60 days the nest was monitored. The male Harpy Eagle delivered 12 prey items to the nest in 29 days (average of 1 delivery every 2.4 days) in the first observation period. He delivered five pale-throated three-toed sloths (*Bradypus tridactylus*), four wedge-capped capuchins (*Cebus olivaceus*), and three unidentifiable prey items. Seven prey deliveries were recorded in 15 days (average 1 delivery every 2.1 days) in the second observation period, four by the male and three by the female. Three of the seven prey delivered were capuchin monkeys, two were sloths, and two could not be identified. Four prey deliveries were observed in 15 days in the third observation period (average 1 delivery every 3.7 days). Two deliveries were made by the male, and the other two were made by the female. It was not possible to identify these prey items as the only video recorded of these deliveries was from positions that did not allow us to see into the nest.

Synchronous Hatching.—Both eggs in the Harpy Eagle nest hatched on the same day (12 May 2009). Two chicks were seen in the nest up to 14 days after hatching, at times seen struggling to climb on top of each other. Only one of the chicks was ever observed being fed by the female at a time, although we could not tell if it was always the same chick.

DISCUSSION

Our observations of Harpy Eagles at the nest suggest that green branch collection is important for nest sanitation. Harpy Eagle behavior in response to arthropods (head shaking and pecking) was much more frequent in the first period of observation than subsequent observation periods suggesting that arthropods were more problematic when the chick(s) were newly hatched. This observation can be explained by a change in arthropod abundance/activity around the nest between different observation periods or, alternatively, the female Harpy Eagle may have been more diligent in removing potentially dangerous arthropods when the chick was very small and

presumably more vulnerable to parasitism or being bitten and stung.

Little is known about the effect of parasites and diseases on Harpy Eagle nestlings. Arthropod ectoparasites such as botflies in the genus *Philornis* can have a highly detrimental effect on survival of nestlings of many bird species in the Neotropics (Dudaniec and Kleindorfer 2006) including small Falconiformes (Delannoy and Cruz 1991). Stinging and biting arthropods such as ants and wasps may also pose a threat to a harpy chick when it is small. Rettig (1978) observed a nesting female Harpy Eagle to snap at and kill insects, particularly bees and wasps that got close to the nest. The female Harpy Eagle in Rettig's (1978) study preferred collecting branches of *Mora* trees rather than those of the *C. pentandra* tree in which it was nesting. These observations suggest high selectivity for particular kinds of green branches, but we could not tell whether this selectivity was based on arthropod-repelling quality or some other factor such as the ease at which the branches could be broken. The 'nest sanitation by repelling insects with volatile components of leaf chemistry' hypothesis cannot be ruled out. However, there was no consistency in branch choice between studies and insects were observed on the nest even when green branches were present (i.e., insect repelling capability of the green branches did not seem to be strong).

The most common prey delivered to the nest in Rettig's (1978) study were sloths and capuchin monkeys. Sloths have been shown to be important components of Harpy Eagle diets in widely different parts of its range including Panama (Touchton et al. 2002) and the Brazilian Amazon (Galetti and de Carvalho 2000). Red-howler monkeys (*Alouatta seniculus*) were common in our study area with several groups living within a 500-m radius of the nest. Red-howler monkeys can be taken by Harpy Eagles (Rettig 1978, Peres 1990, Sherman 1991), and the similar-sized mantled howler (*A. palliata*) is the preferred primate prey of Harpy Eagles on Barro Colorado Island in Panama (Touchton et al. 2002). However, we did not observe any howler remains in the nest.

Rettig (1978) observed a prey delivery rate of one prey every 3.5 days in the first part of the nesting period when the male was doing all the hunting and one prey every 2.5 days later in the nesting period when both adults were hunting. We observed the male Harpy Eagle deliver prey on average once every 2.4 days in the first period, and both parents delivered at an average rate of once every 2.1 days in our second observation period. There are many possible explanations for this apparently higher delivery rate at our study site, including differences in prey abundance or even ease of catching prey. One reason for increased prey delivery could be that the forest fragmentation characterizing our study area resulted in large amounts of forest edge habitats which may be favored by Harpy Eagles hunting monkeys (Eason 1989).

Many eagle chicks show siblicidal behavior, but hatching is usually asynchronous (Simmons 1986) making competition between chicks much more asymmetric. Our observations of synchronous hatching differ from those of Rettig (1978) who only observed one of two Harpy Eagle eggs in the clutch hatch. Our observation is unexpected as more equally-sized competing chicks have a similar potential to damage each other, which could result in the reduced survival of both competitors.

More data are needed to quantify Harpy Eagle behavior and evaluate hypotheses for the adaptive significances of these behaviors. However, unless methods for finding and monitoring Harpy Eagle nests are greatly improved so that large sample sizes can be obtained for reasonable effort, our understanding of Harpy Eagle behavior is likely to remain obscure.

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Screaming Cowbird Parasitism of Nests of Solitary Caciques and Cattle Tyrants

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ABSTRACT.—The Screaming Cowbird (*Molothrus rufoaxillaris*) is one of the most specialized brood parasites with only three known hosts: Baywing (*Agelaioides badius*), the main host throughout most of its range, and two alternative hosts in some areas of its distribution, Chopi Blackbird (*Gnorimopsar chopi*) and Brown-and-yellow Marshbird (*Pseudoleistes virescens*). We studied Screaming Cowbird parasitism in northeast Argentina where this parasite uses Baywings and Chopi Blackbirds as hosts. We monitored 69 nests of Baywings, 251 of Chopi Blackbirds, 31 of Solitary Caciques (*Cacicus solitarius*), and 30 of Cattle Tyrants (*Machetornis rixosa*). The frequency of Screaming Cowbird parasitism on Baywing nests was 80% and was 46% for Chopi Blackbirds. We recorded one event of Screaming Cowbird parasitism on one nest of Solitary Caciques and three events of Screaming Cowbird parasitism on one nest of Cattle Tyrants. The identities of parasitic eggs in both hosts were confirmed by sequencing the mtDNA control region. We propose these events of parasitism resulted from recognition errors by Screaming Cowbird females that regularly parasitize Baywings and Chopi Blackbirds. The nest of Solitary Caciques had been frequently visited by a pair of Baywings before Screaming Cowbird parasitism occurred, and the nest of Cattle Tyrants was near an active Chopi Blackbird nest that had been previously parasitized by Screaming Cowbirds. *Received 5 January 2010. Accepted 7 April 2010.*

The Screaming Cowbird (*Molothrus rufoaxillaris*) is a specialized brood parasite, which exclusively uses the Baywing (*Agelaioides badius*) as a host throughout most of its range (Mason 1980, Fraga 1998). It also parasitizes the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) in some areas (Mermoz and Fernández 2003) and the Chopi Blackbird (*Gnorimopsar chopi*) (Sick 1985, Di Giacomo 2005). Other species have been reported as hosts of the Screaming Cowbird, but there is general agreement that most of these reports were based on mis-identified Shiny Cowbird (*M. bonariensis*) eggs (Friedmann 1963, Mason 1980, Fraga 1986).

One hypothesis posited to explain host specificity in brood parasites is that females imprint on

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their foster parents and, once mature, search for nests of the same species in which to lay their eggs (Nicolai 1964, Slagsvold and Hansen 2001). This hypothesis has been directly supported by experiments with captive brood-parasitic Village Indigobirds (*Vidua chalybeata*) bred in captivity and foster-reared by their normal host or by an experimental foster species and tested as adults for host choice (Payne et al. 2000). Indirect evidence in support of this hypothesis include: (1) the host specificity of Common Cuckoo (*Cuculus canorus*) females, but not males (Marchetti et al. 1998), and (2) the association between host species and parasite's mitochondrial, but not nuclear DNA (Gibbs et al. 2000).

Host imprinting and occurrence of recognition errors when parasitic females search for host nests (i.e., to lay eggs in nests of hosts other than the foster parents) may result in use of new hosts. This may lead to the formation of host specific races, if only females imprint on their hosts as by Common Cuckoos (Gibbs et al. 2000) or in speciation, if both males and females imprint on their hosts (i.e., indigobirds [*Vidua* spp.]; Payne et al. 2002, Sorenson et al. 2003).

Friedmann and Kiff (1985) suggested host imprinting may also occur in cowbirds and individual females may be host specialists. The evidence, however, is controversial for Brown-headed Cowbirds (*M. ater*). One study showed no genetic differentiation in mtDNA between cowbird chicks raised by two different hosts (Gibbs et al. 1997), whereas results from another study at the same site, showed that half of the females laid in nests of a single host (Alderson et al. 1999). MtDNA haplotype frequency distributions in Shiny Cowbirds differed among parasitic chicks from nests of four hosts (Mahler et al. 2007), which indicate the occurrence of a non-random laying behavior by females of this parasite. A recent study (Mahler et al. 2009) of the host specialist Screaming Cowbird, showed that frequency distributions of mtDNA haplotypes differed between cowbird chicks from nests of Baywings and Chopi Blackbirds. This result indicates host choice by females is not random and female Screaming Cowbirds may preferentially parasitize nests of the foster parents. The number of mutations between directly related haplotypes in the latter study was small, which indicates that haplotype divergence in the population is relatively recent in evolutionary terms. Mahler et al. (2009) suggested a few Screaming Cowbirds may have switched recently from Baywings to Chopi Blackbirds, giving rise to a new race that only uses the latter host.

Successful host switches require females to lay eggs in nests of a host other than the foster parent (recognition errors), that the new host successfully rears parasitic females, and these females subsequently use the new foster parent as a host. We present direct evidence through genotyped eggs of Screaming Cowbird parasitism of two new hosts: Solitary Cacique (*Cacicus solitarius*) and Cattle Tyrant (*Machetornis rixosa*). Our study was conducted in an area where Screaming Cowbirds parasitize Baywings and Chopi Blackbirds. We propose parasitism of the new hosts resulted from recognition errors by Screaming Cowbird females that regularly parasitize Baywings and Chopi Blackbirds.

METHODS

Study Area.—The study was conducted at 'Reserva Ecológica El Bagual' in the Province of Formosa, Argentina (26° 18′ 17.5″ S; 58° 49′ 51.1″ W). This reserve is an open savanna of 3,300 ha in the eastern or humid Chaco region. Average annual rainfall at the study site is 1,350 mm and mean monthly temperatures vary from 16.9° C in July to 26.7° C in January.

Data Collection and Analysis.—We monitored nests of potential hosts of Shiny and Screaming cowbirds during the 1997–1998 to 2008–2009 breeding seasons. We found 69 nests of Baywings, 251 of Chopi Blackbirds, 31 of Solitary Caciques, and 30 of Cattle Tyrants. Most nests were found during construction, laying, and incubation, and were visited every 2–3 days until chicks fledged or the nest failed. Individual eggs were marked with waterproof ink and assigned to the host or to Shiny or Screaming cowbirds on the basis of background color, spotting pattern, and shape (Fraga 1983). We also genetically identified 27 and 31 Screaming Cowbird eggs in nests of Baywings and Chopi Blackbirds, respectively, by sequencing the control region of the mtDNA (Mahler et al. 2009). Screaming Cowbird eggs from nests of Solitary Caciques and Cattle Tyrants were also genetically identified. The initial assignment of Screaming Cowbird eggs on the basis of color and spotting pattern was confirmed by genetic analysis in all cases. Frequency of parasitism was calculated as number of nests with parasite eggs or chicks divided by total number of

nests found, and intensity of parasitism as number of parasitic eggs per parasitized nest.

Genetic Identification of Screaming Cowbird Eggs.—We sequenced a 600 base pair fragment of the mtDNA control region using primers MBO-L1 and MBO-H2 (Mahler et al. 2007). We collected Screaming Cowbird eggs and artificially incubated them for 48 hrs to obtain some embryonic development. We kept eggs at −20° C until they were processed. Embryonic tissue was obtained from the eggs and stored in DMSO buffer for posterior DNA extraction following a standard ethanol protocol (Miller et al. 1988). PCR reactions were performed as described by Mahler et al. (2009). We sequenced the amplified products on an Applied Biosystems Model 3100 Genetic Analyzer using ABI Big Dye™ Terminator Chemistry. We compiled the sequences in Bioedit Version 7.0.5.3 software (Hall 1999) and compared them with those deposited in the EMBL, GenBank, under accession numbers EU199785-EU199795 (Mahler et al. 2009).

RESULTS

Screaming Cowbirds regularly parasitized Baywings and Chopi Blackbirds at our study site. The frequency of parasitism of Baywing nests was 80% (n = 69 nests) with an intensity of parasitism of 2.4 ± 0.2 eggs per parasitized nest ($\bar{x}$ ± SE, n = 51 nests). Frequency and intensity of parasitism of Chopi Blackbird nests were 46% (n = 251 nests) and 3.0 ± 0.2 eggs (n = 116 nests), respectively.

Shiny Cowbirds parasitized only one of 31 nests of the Solitary Cacique (3%). We recorded one event of Screaming Cowbird parasitism in one nest of Solitary Caciques in December 2007. Baywings had visited this nest several times during the previous days and had tried, unsuccessfully, to usurp the nest. Screaming Cowbird parasitism occurred before host laying and, after parasitism, the caciques deserted the nest. The egg was collected and incubated, DNA extracted, and the control region sequenced. The sequence of the mtDNA control region corresponded to Screaming Cowbirds' haplotype H5 (Mahler et al. 2009).

We also monitored 30 nests of Cattle Tyrants but Shiny Cowbirds parasitized none of them. We recorded three events of Screaming Cowbird parasitism of one Cattle Tyrant nest during laying in November 2008. This nest was <1 m from an active Chopi Blackbird nest that was also multiple parasitized by Screaming Cowbirds. Cattle Tyrants incubated the Screaming Cowbird's eggs of which one hatched but the chick disappeared from the nest 48–72 hrs after hatching. We collected the other two eggs, one of which was rotten and we could not extract DNA from it. The sequence of the mtDNA control region of the other egg corresponded to Screaming Cowbirds' haplotype H1 (Mahler et al. 2009).

DISCUSSION

We confirmed Screaming Cowbird parasitism of two new hosts, Solitary Cacique and Cattle Tyrant, in an area where this parasite regularly uses Baywings and Chopi Blackbirds. Solitary Caciques and Cattle Tyrants were previously reported as parasitized by Shiny Cowbirds, but until now they had not been mentioned as parasitized by Screaming Cowbirds (Ortega 1998). We propose these parasitism events resulted from recognition errors by female Screaming Cowbirds that regularly parasitize Baywings and Chopi Blackbirds. A pair of Baywings had frequently visited the nest of Solitary Caciques before Screaming Cowbird parasitism occurred, and the nest of the Cattle Tyrants was near an active nest of Chopi Blackbirds that had been previously parasitized by Screaming Cowbirds.

Baywings seldom build nests but rather exploit a wide variety of covered nesting sites, including old nests built by other species and holes in trees (Fraga 1988, De Mársico et al. 2010). Baywings at our study site usually use old nests of Greater Thornbirds (*Phacellodomus ruber*) and Little Thornbirds (*P. sibilatrix*) but, at times they usurp and use nests of Solitary Caciques and becards (*Pachyramphus* spp.) (Di Giácomo 2005). This may promote recognition errors by Screaming Cowbird females searching for nests occupied by its main host. Baywings also use holes in trees, which may have favored colonization of hole-nesting Chopi Blackbirds.

The first step in the process of colonization of a new host would be occurrence of recognition errors when parasitic females search for host nests (i.e., to lay eggs in nests of a host species other than their foster parents). We show this type of error may occur at low frequencies in Screaming Cowbirds. However, the low frequency of parasitism of Solitary Caciques and Cattle Tyrants also suggests the other steps necessary for parasitism of a new host (i.e., rearing parasitic females that subsequently use the same species as

a host; Payne et al. 2000, 2002; Sorenson et al. 2003) have not yet occurred in these hosts. The three known hosts of Screaming Cowbirds (Baywings, Chopi Blackbirds, and Brown-and-yellow Marshbirds) are cooperative breeders (Orians et al. 1977, Fraga 1991, Di Giacomo 2005), which suggests competition for food with nest mates is critical for Screaming Cowbirds. Thus, this parasite has only been successful in hosts' nests where competition is less intense, as breeding pairs have one or more helpers at the nest that contribute to chick provisioning (De Mársico and Reboreda 2008). This hypothesis requires further investigation.

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Snakes are Important Nest Predators of Dickcissels in an Agricultural Landscape

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ABSTRACT.—We used video cameras to monitor 33 Dickcissel (*Spiza americana*) nests during 2003–2004 in the highly-fragmented, agricultural ecosystem of eastern Nebraska and western Iowa. Nine nests fledged young, 20 were completely depredated, three were partially depredated, and one was abandoned due to ants. Nine snakes, six small mammals, six common raccoons (*Procyon lotor*), two Brown-headed Cowbirds (*Molothrus ater*), and one American mink (*Neovison vison*) were documented as nest predators. These results suggest a diversity of predators is responsible for depredation of Dickcissel nests with snake predation being an important cause of nest failure. *Received 21 December 2009. Accepted 24 May 2010.*

Nest predation is the leading cause of reproductive failure for many bird species across numerous regions and habitats (Martin 1993), and may be an important factor in avian population declines (Heske et al. 2001). Grassland birds are of special concern because they have undergone declines greater than any group of birds in North America (Knopf 1994) and have shown decreasing reproductive rates with increased habitat fragmentation (Herkert et al. 2003). Nearly 80% of grasslands in the Great Plains of North America have been converted to agricultural use, and <4% of the tallgrass prairie remains (Samson and Knopf 1994). Grassland birds nesting in the remaining grasslands often experience low reproductive success due to landscape features in agroecosystems that attract a diversity of nest predators (Bergin et al. 2000).

Previous studies have identified predators of grassland bird nests, but more studies are necessary to understand how predator communities differ among regions and what factors may contribute to these differences (Weatherhead and Blouin-Demers 2004). At least two video studies of nesting birds that have occurred in North American grasslands were in areas that could be considered tallgrass prairie, but were conducted at the edge of the historical tallgrass prairie range. Thompson and Burhans (2003) documented predators of shrub-nesting birds in old fields in Missouri, and Renfrew and Ribic (2003) documented predators of five grassland species in grazed pastures in the Driftless Area of Wisconsin; both studies were conducted along the ecotone with eastern deciduous forests. Pietz and Granfors (2000) studied nest predation on 10 species of grassland passerines and Grant et al. (2006) studied two passerine species in mixed-grass prairie in North Dakota. To date, no studies have been conducted in the highly fragmented, agricultural ecosystem in the core of the former tallgrass prairie biome. Our objective was to identify predators of Dickcissel (*Spiza americana*) nests within small grassland patches interspersed within intensive row crop agriculture. Dickcissels are of conservation concern and have shown

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TABLE 1. Nest predators recorded on video with corresponding number of Dickcissel nests depredated at incubation and nestling stages.

Predator	Incubation	Nestling	# Events
Snakes			
Fox snake (*Elaphe vulpina*)	3	2	5
Plains garter snake (*Thamnophis radix*)	0	2	2
Eastern yellowbelly racer (*Coluber constrictor flaviventris*)	0	1	1
Bullsnake (*Pituophis catenifer*)	1	0	1
Small mammals			
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	2	1	3
Franklin's ground squirrel (*S. franklinii*)	0	1	1
Cricetid rodent (*Peromyscus* spp.)	2	0	2
Mid-sized mammals			
Common raccoon (*Procyon lotor*)	4	2	6
Other			
Brown-headed cowbird (*Molothrus ater*)	1	1	2
American mink (*Neovison vison*)	0	1	1
Totals	13	11	24

population declines similar to other grassland passerines, but their predator community has not been documented on video. Dickcissels are an ideal model for understanding how nest predator communities vary among regions, landscapes, or habitat types because they inhabit marginal grasslands in extremely fragmented landscapes as well as relatively unfragmented landscapes.

METHODS

We monitored Dickcissel nests at DeSoto National Wildlife Refuge, Boyer Chute National Wildlife Refuge, Allwine Prairie Preserve, Cuming City Cemetery and Nature Preserve, and a privately owned Conservation Reserve Program (CRP) parcel in eastern Nebraska and western Iowa (Klug et al. 2009). The grasslands were managed with prescribed burning but no livestock grazing. Vegetation in the grasslands was either dominated by native warm-season grasses or by exotic cool-season grasses with variation in forb density (Klug 2005). We video-documented predators of Dickcissel nests in 15 grassland fragments ranging from 4 to 45 ha ($\bar{x}$ ± SE = 20.3 ± 3.1). The landscape within 1,600 m of grassland fragments included six major land cover types based on the evaluation of orthophotographs in ArcMap GIS (scale of 1:1500) by Klug et al. (2009). We classified the landscape as an agroecosystem because 20–64% ($\bar{x}$ ± SE = 52.5 ± 3.9) of the surrounding land was in crop production (e.g., corn or soybeans). Grasslands covered 2–43% ($\bar{x}$ ± SE = 17.8 ± 2.5) and trees 6–42% ($\bar{x}$ ± SE = 15.7 ± 2.5) of the landscape. Human development covered 0.5–22% ($\bar{x}$ ± SE = 4.0 ± 1.7), and roads <2% ($\bar{x}$ ± SE = 1.2 ± 0.1), whereas wetlands and water bodies covered 1–14% ($\bar{x}$ ± SE = 5.4 ± 1.0) of the landscape.

We used 24-hr time-lapse video systems to monitor nests and identify predators removing or consuming eggs and nestlings. We constructed six battery-powered video systems, which included a camera (V-1214-IR Weatherproof Bullet Camera with infrared illumination, Marshall Electronics, El Segundo, CA, USA) attached to a time-lapse video recorder (SSC-960 Time Lapse VCR, Samsung Electronics America Inc., Ridgefield Park, NJ, USA) by 8.5 m of cable (buried under vegetation and litter) and powered by a sealed lead acid battery connected by a power converter (375w PowerVerter, Tripp-Lite World Headquarters, Chicago, IL, USA). The camera was attached to a wood dowel and placed within 10 cm of the nest so the camera was completely obscured by vegetation, but vegetation did not completely obscure the field of view. We minimized disturbance at the nest by setting up the system in <20 min between 1000 and 1600 CST, in dry, moderate temperatures. We set up systems during both incubation and nestling stages, but only after females had incubated for 3–5 days to minimize abandonment. Nest contents were checked re-

TABLE 2. Nest predators of grassland passerines documented on video in Nebraska/Iowa, North Dakota, Missouri, and Wisconsin.

Predator	Nebraska Iowa[a]	North Dakota[b]	North Dakota[c]	Missouri[d]	Wisconsin[e]
Snake (*Elaphe vulpina*, *E. obsoleta*, *Thamnophis* spp., *Coluber constrictor*, *Lampropeltis getula*, *L. calligaster*, *Pituophis catenifer*)	9		2	33	3
Common raccoon (*Procyon lotor*)	6		1	4	8
Squirrel (*Spermophilus tridecemlineatus*, *S. franklinii*, *Sciurus niger*)	4	13	11	1	4
Brown-headed Cowbird (*Molothrus ater*)	2	2	5	1	1
Mouse or vole (*Peromyscus* spp., *Zapus* spp., *Microtus* spp.)	2	2	3	2	
Long-tailed weasel/American mink (*Mustela frenata*, *Neovison vison*)	1	1		1	
American badger (*Taxidea taxus*)		2	3		2
Bird of prey (*Buteo* spp., *Circus cyaneus*, *Tyto alba*)		2	1	3	2
Red fox/coyote/domestic dog (*Vulpes vulpes*, *Canis latrans*, *C. lupus familiaris*)		2			1
Domestic cat (*Felis catus*)					1
Striped skunk (*Mephitis mephitis*)					1
Virginia opossum (*Didelphis virginiana*)					1
White-tailed deer (*Odocoileus virginianus*)		2	2		
Unidentified		1	2	1	
Totals	24	27	30	46	24

[a] This study.
[b] Pietz and Granfors (2000).
[c] Grant et al. (2006).
[d] Thompson and Burhans (2003).
[e] Renfrew and Ribic (2003).

motely by attaching a portable monitor to the system every 24 hrs given that the tape ran out after 24 hrs. We archived the tape to identify the predator using a high-resolution monitor and slow motion function if the contents differed from the previous day. We recorded time, nest stage, nest contents, and contents removed for each depredation event.

We estimated daily survival rates (DSR) for nests using Program MARK with the design matrix tools and the logit-link function (Dinsmore et al. 2002), and calculated variance using the Delta method (Powell 2007). We also estimated DSR for nests without video systems to better understand the influence of the equipment on nest survival. Means ± SE are presented.

RESULTS

We video-monitored 33 nests over 2 years (2003 = 15 nests, 2004 = 18 nests) for 287 observation days during incubation (n = 148 days) and nestling (n = 139 days) stages. Nests were monitored an average of 12.9 ± 1.0 days. We placed cameras at 19 nests that recorded both incubation and nestling stages, 11 nests during the incubation stage only, and three nests during the nestling stage only. The DSR of nests monitored with video was 0.946 ± 0.01 for an overall survival of 0.333 ± 0.07 if we extrapolated to a 20-day nesting cycle (i.e., the average length of a Dickcissel nesting cycle). The probability of predation for nests with cameras was similar to nests not monitored with video systems (DSR = 0.934 ± 0.005, overall survival rate = 0.255 ± 0.03). Twenty of the nests monitored completely failed due to depredation, three nests were partially depredated before eventual fledging of young, nine nests fledged young with no depredation, and one nest was abandoned after an ant infestation.

Nine snakes, six small mammals, six common raccoons (*Procyon lotor*), two Brown-headed Cowbirds (*Molothrus ater*), and one American mink (*Neovison vison*) were documented as nest predators (Table 1). We documented one instance of a multiple predation at one nest (i.e., a Brown-headed Cowbird removed three Dickcissel eggs prior to a thirteen-lined ground squirrel [*Spermophilus tridecemlineatus*] consuming the remaining 2 Brown-headed Cowbird and 1 Dickcissel egg). We documented partial predation by a fox snake (*Elaphe vulpina*) late in the nesting cycle at two nests, which caused the surviving nestlings to fledge prematurely. A fox snake at another nest was documented consuming one egg and leaving three, which later hatched and fledged. We

observed one female Brown-headed Cowbird removing Dickcissel nestlings without laying eggs. We recorded 13 and 11 depredations at the incubation and nestling stages, respectively (Table 1). Depredation by cricetid rodents and raccoons were nocturnal, whereas depredation by ground squirrels, mink, and cowbirds were diurnal. All depredations by snakes were diurnal except two by fox snakes, which were nocturnal.

DISCUSSION

The potential predator community in agricultural systems is diverse; thus, the composition of the community, and identity of the dominant predator, will ultimately dictate nest predation risk (Klug et al. 2009). We found at least 10 species responsible for predation of Dickcissel nests, including both obligate grassland species (e.g., ground squirrels and snakes) and more wide-ranging habitat generalists (e.g., common raccoon and Brown-headed Cowbird; Table 1). Our sample size of video-monitored nests (n = 33) is consistent with other studies in the grasslands of North America (Table 2), but it is likely that additional predator species would be detected with a larger sample size. For example, striped skunk (*Mephitis mephitis*), Virginia opossum (*Didelphis virginiana*), American Crow (*Corvus brachyrhynchos*), and coyote (*Canis latrans*) have been documented as nest predators (Renfrew and Ribic 2003, Peterson et al. 2004, Staller et al. 2005), but were not documented at our study sites regardless of their presence on predator surveys (Klug et al. 2009). However, given the consistency of snake events across years, it is unlikely a larger sample would change our conclusion that snakes are among the most important nest predators for grassland birds in this region.

Information about the predator community is important for understanding variation in nest predation and to increase productivity of nesting birds (Lahti 2009). However, recognizing the importance of the predator community also brings challenges. Studies that document predation of grassland bird nests consistently discover wide-ranging generalist predators including Brown-headed Cowbird and common raccoon. Thus, efforts directed at increasing reproductive success of birds have often focused on decreasing the population size of species that have increased due to agricultural land use (Heske et al. 1999, Kosciuch and Sandercock 2008). Our study, and other nest predation studies in grassland habitats, has revealed considerable nest predation by snakes and ground squirrels, which are essential members of prairie communities (Table 2). Recommendations directed at decreasing the influence of resident predators in grasslands where birds are nesting are not straightforward given that many of these species are also targets of conservation. For example, fox snakes and Franklin's ground squirrels (*Spermophilus franklinii*) are native members of the tallgrass prairie (Martin et al. 2003) and efforts to control these predators to increase bird populations must proceed with caution.

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Interspecific Cavity-sharing Between a Helmeted Woodpecker (*Dryocopus galeatus*) and Two White-eyed Parakeets (*Aratinga leucophthalma*)

Kristina L. Cockle[1,2,3]

ABSTRACT.—Cavity-nesting birds may frequently eompete for a limited supply of nest and roost cavities in trees, but interspecifie sharing of these eavities has rarely been reported. The globally vulnerable Helmeted Woodpecker (*Dryocopus galeatus*), a little-known Atlantic Forest endemic, is believed to be threatened by nest-site competition; however, little is known about its eeology or natural history. I report an observation of a female Helmeted Woodpeeker roosting with two White-eyed Parakeets (*Aratinga leucophthalma*) in their non-exeavated (natural) nest cavity at Cruee Caballero Provineial Park, Argentina, and diseuss possible implieations for eeology and conservation of this rare woodpecker. *Received 22 January 2010. Accepted 20 April 2010.*

Tree cavities are used by many bird species for nesting and roosting, and supply of cavities may be a key resource that limits populations (Newton 1994) and structures communities (Martin et al. 2004, Aitken and Martin 2008). Compctition within specics for a limited supply of cavities may lead to physical conflict resulting in injuries to adults and dcath of their young (Snyder et al. 1987, Heinsohn and Legge 2003). Cavity limitation may also create conditions that favor coopcrative brccding (Heinsohn and Legge 2003). Cavity usurpation is common among competing species (Snyder et al. 1987, Renton and Brightsmith 2009, Strubbe and Matthysen 2009), but cavities could also be shared between species (Robinson et al. 2006). Interspecific cavity-sharing would allow individuals to avoid costs associated with aggressive usurpation of cavities.

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Sharing could also provide benefits including predator vigilance.

The Helmeted Woodpecker (*Dryocopus galeatus*) is rare, little-known, globally vulnerable, and endemic to the Atlantic Forest of Paraguay, Argentina, and Brazil (BirdLife International 2008). It is considered a bird of tall forests (Winkler et al. 1995) and may be most common in mature forest in the Province of Misiones, Argentina (Bodrati and Cockle 2006). Little else is known about its natural history or ecology, but competition for nest sites with the larger and more abundant Lineated Woodpecker (*D. lineatus*) has been proposed as a key threat (BirdLife International 2008).

OBSERVATIONS

I observed a female Helmeted Woodpecker roosting overnight with a pair of White-eyed Parakeets (*Aratinga leucophthalma*), while the latter were incubating in a naturally occurring, non-excavated cavity in a large live branch of grapia (*Apuleia leiocarpa*). The site was in Cruce Caballero Provincial Park (26° 31′ S, 53° 58′ W), Province of Misiones, Argentina, in primary mixed Atlantic Forest with laurel (*Nectandra* and *Ocotea* spp.), guatambú (*Balfourodendron riedelianum*), and Paraná pine (*Araucaria angustifolia*) (Cabrera 1976). The Helmeted Woodpecker is scarce in the park, and the White-eyed Parakeet is abundant (Bodrati et al. 2010). A pair of White-eyed Parakeets laid at least two eggs in the cavity in December 2008 (Cockle et al. 2010), but their nest failed. The cavity was empty when checked for contents on 21 October and 2 November 2009.

The cavity was shared for at least two consecutive nights on 3 and 4 December 2009 by a Helmeted Woodpecker and a pair of White-eyed Parakeets. The cavity contained one white egg on 3 December 2009. The following day, I arrived at the cavity at 0520 hrs, 20 min before dawn. The sky was dark, cloudy, and threatening to rain. A female Helmeted Woodpecker appeared from inside the cavity at 0525 hrs. She remained at the cavity entrance until 0537 hrs when she flew out, clung briefly to the roots of an epiphytic güembé (*Philodendron* spp.) about 2 m distant, then returned to the cavity. She remained in or near the cavity entrance until 0752 hrs and I could clearly distinguish her brown face from the chin to above the eye. She left the cavity three times to peck at the güembé roots or move up the branch within 1 m of the cavity entrance. Three times she seemed to glean insects just inside the cavity entrance. She did not descend to the floor of the cavity (egg chamber) and remained visible just inside the entrance. It rained from 0616 to 0625 hrs but the sun shone directly on the cavity from 0712 hrs onwards. At 0752 hrs the woodpecker became agitated, jumping forward and backward inside the cavity. She flew out of the cavity and disappeared into the forest. Two White-eyed Parakeets immediately emerged from the bottom of the cavity and flew away in silence. Neither the woodpecker nor the parakeets vocalized that morning, and there was no sign of aggression.

I returned to the cavity at 0510 hrs the following day accompanied by A. A. Bodrati. The sky was clear and the nest tree was illuminated by bright moonlight. We could immediately see the Helmeted Woodpecker in the cavity, apparently awake. She flew from the nest cavity 10 min before sunrise at 0530 hrs. The two White-eyed Parakeets emerged immediately from the bottom of the nest. They stayed 6 min at the entrance and then flew away in silence.

The cavity was 12.4 m above ground in a live healthy grapia that measured 30 m in total height and 87 cm in diameter at breast height. It had one lateral entrance 6 cm wide × 38 cm tall. The cavity was 90 cm deep vertically and 14 cm deep horizontally. An epiphytic güembé higher on the branch was rooted inside the cavity. I believe the parakeets roosted in the egg chamber and incubated the egg, and the woodpecker roosted above them near the cavity entrance.

J. M. Klavins showed me another roost cavity at Cruce Caballero Provincial Park used by a Helmeted Woodpecker in May 2005. That cavity seemed to have been formed where a branch broke off the tree, and either a woodpecker excavated the knot-hole or the cavity formed through decay processes. It was about 12 m high in the main trunk of a live healthy tree, 59 cm in diameter, 24 m tall, at the edge of the park. It was later occupied by a nest of bees in 2006–2007, a roosting male Lineated Woodpecker in 2008 and 2009, and a successful nest of Scaly-headed Parrots (*Pionus maximiliani*) in 2009 (KLC and J. M. Lammertink, unpubl. data).

DISCUSSION

Reports of interspecific cavity-sharing are uncommon. Skutch (1969) reports a cavity in Central America to which a pair of Streak-headed Woodcreepers (*Lepidocolaptes souleyetii*) and a

Tawny-winged Woodcreeper (*Dendrocincla anabatina*) brought nest material alternately; the Tawny-winged Woodcreeper incubated the two eggs and raised the single nestling, a Streak-headed Woodcreeper. Robinson et al. (2006) report a mixed brood of Red-breasted Nuthatches (*Sitta canadensis*) and Mountain Chickadees (*Poecile gambeli*) raised in the same cavity by parents of both species in North America. I observed several incidences of probable interspecific nest-usurpation during four breeding seasons studying cavity-nesting birds in the Atlantic Forest, but this is the first time I observed simultaneous interspecific cavity-sharing among birds, and it appears to be the first such report for South America.

Much remains to study about the role of tree cavities in the ecology and conservation of the Helmeted Woodpecker (Winkler et al. 1995). Apparent nests were reported in a cavity 7.8 cm in diameter, 2.3 m high in an unidentified tree at Iguazú National Park in Misiones in spring 1985 (adults seen entering and leaving cavity without food) and by the side of a road in adjacent Iguaçu National Park in Brazil in November 1988, but no further descriptions are available (Collar et al. 1992; Chebez 1994; Winkler et al. 1995; Hernán Casañas, pers. comm.). A photograph of the first cavity by Martín Adamovsky (published in Chebez 1994) shows it to have a circular entrance, apparently excavated by a woodpecker. Juan Mazar Barnett (pers. comm.) reported a male quietly excavating a cavity in a dead branch of a live laurel (*Nectandra* spp.) tree at Puerto Peninsula, Misiones, on 31 October 1994. A female was nearby at times, always passive, and did not excavate. Madroño Nieto and Esquivel (1995) reported two pairs nesting in spring 1994 at Reserva Natural del Bosque Mbaracayú in Paraguay without further details.

The roost hole shared with the White-eyed Parakeets was not excavated by a woodpecker. The Helmeted Woodpecker has a narrow-based, weak-tipped bill and forages mainly by scaling and pecking (Brooks et al. 1993). Further studies may find that Helmeted Woodpeckers frequently reuse old cavities, entering into competition with secondary cavity-nesting birds such as parrots. Cavities may be in short supply in the Atlantic Forest: high-grade logging has already removed the largest trees with the greatest potential for cavity formation from nearly all remaining forest (Cockle et al. 2010).

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Response to Nestling Throat Ligatures by Three Songbirds

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Chris Kirkpatrick,[1] and Dominic D. LaRoche[1]

ABSTRACT.—We attempted to collect diet samples using throat ligatures from nestlings of three songbird species in a riparian woodland in southeastern Arizona from May to August 2009. We had success with Song Sparrows (*Melospiza melodia*), observed adult Yellow-breasted Chats (*Icteria virens*) reclaim food from nestlings, and discontinued the use of throat ligatures when we observed an adult Abert's Towhee (*Pipilo aberti*) remove two, 3–4-day-old ligatured nestlings from its nest. Previous studies have reported problems (e.g., aggression toward nestlings by adults) with throat ligatures, but we are the first to document removal (and subsequent nestling mortality) in response to this technique. We urge investigators to exercise caution when using throat ligatures on species for which evidence of the safety and efficacy of this method are lacking, especially when nestlings are small in size relative to adults. *Received 18 February 2010. Accepted 29 April 2010.*

Documenting the diet of birds is an important component of many studies designed to test hypotheses related to ecology and evolution of birds. Documenting the diet of nestling birds in an unbiased manner is particularly challenging, especially when investigators want to identify prey items to taxonomic levels beyond Order or want precise estimates of biomass. Investigators have used throat ligatures to collect diet samples from nestling birds since the 1930s (Kluijver 1933, Owen 1956, Mellott and Woods 1993). Fecal analysis, the use of artificial nestlings to collect food, analysis of stomach contents, and visual observation (Evans 1964) are often less effective or more invasive than throat ligatures. However, researchers have experienced several problems with throat ligatures related to both quality of the sample obtained and safety of the nestlings sampled. For example, food may slip past the ligature if the ligature is too loose (Owen 1956, Orians 1966), or food is disgorged if the sampling period is too long or the rate of provisioning too high (Orians 1966, Johnson et al. 1980). Moreover, parents will, at times,

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remove and eat the food from the mouth of the ligatured nestling (Robertson 1973). Ligatures have also been found to affect normal gaping (Johnson et al. 1980) and begging behavior (Orians and Horn 1969), and to occasionally cause death by strangulation (Moore 1986, Mellott and Woods 1993).

Several authors have described accounts of aggressive behavior by adults toward nestlings with throat ligatures. Robertson (1973) mentions that Red-winged Blackbirds (*Agelaius phoeniceus*) in a few cases attempted to remove ligatures from nestlings. Little et al. (2009) reported that adult Bobolinks (*Dolichonyx oryzivorus*) pecked and pulled at nestlings' throat ligatures at most nests sampled. Furthermore, aggressive behavior by adults such as grasping the ligature and forcibly pulling the nestlings' heads upwards or sideways occurred at half of the nests. Despite this aggression, Little et al. (2009) did not observe any nestling mortality resulting from the behavior of the adults. We provide the first documentation of nestling mortality resulting from removal by adults of nestlings outfitted with throat ligatures.

METHODS

We monitored nests of Abert's Towhees (*Pipilo aberti*), Yellow-breasted Chats (*Icteria virens*), and Song Sparrows (*Melospiza melodia*) from May to August 2009 in a riparian woodland along the Santa Cruz River at Tumacacori National Historic Park (31° 34′ 03″ N, 111° 03′ 03″ W), Santa Cruz County, Arizona, USA. The elevation is ~1,000 m and the plant communities are cottonwood-willow (*Populus-Salix*) riparian forest along the river and mesquite-hackberry (*Prosopis-Celtis*) woodland in the adjacent upland. We attempted to collect diet samples from nestlings of the focal species by attaching throat ligatures via the collar method (Kluijver 1933, Johnson et al. 1980). We constructed ligatures from 20–22 gauge, solid-core, black or blue plastic-coated copper wire (RadioShack Corp., Forth Worth, TX, USA) and bent the wire into a U-shape which we fitted around the nestlings' necks sufficiently tight to prevent swallowing but sufficiently loose to allow normal breathing and gaping behavior. We weighed (g) each nestling before applying the ligature and returned nestlings to their nest within 10 min. We used binoculars to observe each sampled nest from a distance of ~15 m until we saw adults return with food. We approached the nest after each feeding visit to remove food from the nestlings' mouths with tweezers. We tried to collect samples for 2–4 consecutive feedings at each nest before removing the ligatures to maximize the size of the food sample, and to prevent handling the nestlings and disturbing the nest on more than one occasion. We compensated for the missed feedings during sampling by feeding each nestling a comparable portion of waxworms (pyralid larvae) after we removed the ligatures.

RESULTS

All three nests with ligatured Song Sparrow nestlings (3–8 days of age) yielded diet samples with no apparent problems. We observed adults at four of five Yellow-breasted Chat nests (nestlings of 2–5 days of age) remove food from ligatured nestlings' mouths before leaving the nest when the food was not swallowed (i.e., diet samples were biased; *sensu* Robertson 1973). We sampled (with black ligatures) our first Abert's Towhee nest containing two 3–4-day-old nestlings on 29 July 2009 at 1052 hrs (MST). Nestling "A" weighed 7.0 g and nestling "B" weighed 16.7 g. Both adults arrived at the nest with food ~25 min after we applied the ligatures, and attempted to feed the nestlings for 2–3 min. We observed at least one of the adults consume food that was originally placed in a nestling's mouth, similar to that observed for Yellow-breasted Chats. We approached the nest to collect diet samples after the adults left and found that only nestling "B" remained in the nest. We searched under the nest but could not find nestling "A." We took a diet sample from nestling "B" and retreated to observe the nest from a distance. An adult returned to the nest ~10 min later with food and spent ~1 min trying to feed the nestling. We then watched the adult remove the nestling from the nest and depart from the nest before we lost sight of the adult. We immediately approached the nest, began searching for nestling "B," and found nestling "B" 2 m from the nest on the ground. The ligature was missing, and we concluded the adult had carried the nestling by grasping the ligature thereby forcing the ligature to open and slide off the nestling's neck. We examined nestling "B," found no sign of injury, returned it to the nest, and moved away for observation. The adult returned about 5 min later to feed the nestling and then shaded the nestling for about 5 min. The adult appeared to resume typical behavior as soon as the ligature was removed

from the remaining nestling, suggesting the ligature elicited the adult's response and not the nestling itself. We did not find nestling "A" and assumed that it died after being removed from the nest.

DISCUSSION

Nest sanitation is the process by which parent birds rid their nests of foreign debris (Welty 1982). Several authors have described parent birds attempting to sanitize (remove) banded nestlings when parents perceived leg bands as foreign debris in the nest (Lovell 1945, Berger 1953, Brackbill 1954). No published account exists of a throat ligature eliciting nestling removal by adults despite the superficial resemblance of throat ligatures to leg bands on nestling birds. This behavior has been observed with Florida Scrub-Jays (*Aphelocoma coerulescens*) (Reed Bowman, Archbold Biological Station, pers. comm.). Ours is the first study to report an instance of nestling removal by adults (and subsequent nestling mortality) in response to use of throat ligatures.

We believe other researchers that have reported aggressive behavior of adults toward ligatured nestlings did not observe removal of young because adults in these studies were physically incapable of removing nestlings due to the relative mass of the nestlings. For example, Little et al. (2009) described aggressive behavior (but not removal) of ligatured, 6-day-old Bobolink nestlings that would have weighed 53% of adult body mass (Martin and Gavin 1995). Towhee nestlings in our study were 16 and 37% of adult body mass based on average adult body mass of 44.7 g (Tweit and Finch 1994). Nest substrate may also affect an adult's ability to successfully remove nestlings from a nest and may explain interspecific variation in this behavior.

We encourage future investigators to observe parental behavior at several nests before they use throat ligatures widely on a species for which evidence of the safety and efficacy of this method is lacking, especially on younger nestlings that weigh <50% of adult body mass. Some species accept throat ligatures without problems (e.g., Song Sparrows in our study) and other species experience problems that may bias diet samples (e.g., Yellow-breasted Chats in our study). The color or type of material used to make ligatures may affect the probability of removal and deserves further study. We used both black and blue ligatures, but birds may respond differently to other colors similar to the way that some birds respond differently to different band colors (Burley 1988). We are concerned that removal of young by adults in response to use of throat ligatures on nestlings may be relatively widespread in birds based on recent observations of this behavior by Florida Scrub-Jays (Reed Bowman, pers. comm.), the observations described here of Abert's Towhees, and the recent report of aggression toward ligatured nestlings by Bobolinks (Little et al. 2009).

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William and Nancy Klamm Service Award for 2010: Jerome A. Jackson

In 1971, a young ornithologist presented his first paper at a Wilson Ornithological Society meeting on Dauphin Island, Alabama. This first paper compared the breeding biology of Red-bellied (*Melanerpes carolinus*) and Red-headed (*M. erythrocephalus*) woodpeckers; thus his passion for woodpeckers and his enthusiasm for the Wilson Ornithological Society have been intertwined from early in his ornithological career.

Jerry Jackson's work for the Society has been as extensive as it was varied. In 1973 Jerry was elected Treasurer, succeeding Bill Klamm in the position. Bill mentored Jerry during that year and Jerry's continuing friendship with the Klamms was largely responsible for their bequest to the Society's endowment. He served 1 year as Treasurer before he was elected Editor of the *Wilson Bulletin*, a position he held for 4 years. In 1979 he was elected Second Vice-President, and he rose through the ranks to serve as President from 1983 to 1985. He has hosted not one, but two Wilson Society meetings: one at Mississippi State University in 1977 and another at Florida Gulf Coast University in 2002.

Another of Jerry's passions is history. In 1988, Harold Mayfield, George Hall, and Jerry wrote a history of the Wilson Ornithological Society to mark its first century. Jerry's account of the last third of the first century not only summarized the

growth of the *Wilson Bulletin* and the Society's grants and prizes, but also included anecdotes that provide a flavor of the Society and the people who shaped it during that time. In that paper, Jerry wrote about his tenure as Treasurer, saying "Quite honestly, I was out of my element!" As well as writing about the history of the Society, Jerry himself has shaped it through his long tenure on the nominating committee, his more than three decades of active participation on the Wilson Council, and his work on the conservation, history and archives, and Klamm committees.

With sincere gratitude and great affection, we are proud to present the 2010 William and Nancy Klamm Service Award to Jerome A. Jackson for his four decades of service to the Wilson Ornithological Society.—Sara R. Morris, Richard C. Banks, Robert C. Beason, Robert L. Curry, and E. Dale Kennedy (Klamm Service Award Committee).

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Ornithological Literature

Robert B. Payne, Book Review Editor

MOMENTS OF DISCOVERY. NATURAL HISTORY NARRATIVES FROM MEXICO AND CENTRAL AMERICA. Edited by Kevin Winker. University Press of Florida, Gainesville, Florida, USA. 2010: 384 pages, 50 black and white illustrations. ISBN: 978-0-8130-3417-1. $ 75.00 (hardcover).—This book, edited by Kevin Winker and authored by some of the most outstanding and prolific ornithologists and mammalogists of the 20th century in the northern Neotropics, covers a set of memories, experiences, and points of views of field work in Central America. It also contains what might be the last writings of some charismatic explorers including Miguel Álvarez del Toro, the Coffeys (Ben and Lula), Charles Sibley, John Emlen, and Dwain Warner. Twenty contributions that narrate field adventures that roughly cover from the late 1930s to the 1990s are presented almost unedited. Most of the chapters refer to field collecting experiences in Mexico, understandable in terms of closeness and access for USA-based researchers during the 20th century. However, a handful depicts experiences in Belize, Guatemala, Costa Rica, Panama, and El Salvador.

Field work constitutes possibly the most charming part of an ornithologist's life and, for the vast majority of researchers, the first touch of a foreign fauna becomes an enchanting and breath-taking experience. Therefore, after the confrontation to a new culture, new food, new friends and colleagues, and the addictive combination of fear, excitement, and especially an awesome tropical fauna, everything together and surrounded by an unknown language, most get their hearts trapped in the tropics; sometimes literally because some of the authors even married Latin American women!

The book might seem a kind of anthology, as I am sure it was intended. However, it is much more than the transcription of the stories that otherwise you would only hear around the fireplace in a camp, and joined by a series of tequila shots. After a careful reading it is clear the collection of papers represents very important moments in natural sciences, because among the lines one discovers the intricate system of interrelationships among ornithological research groups, and individuals that started in the post-second world war period and flourished well beyond the 1970s.

For a person passionate about the history of ornithological exploration, like me, the book helps us understand diverse aspects of the sometimes cryptic development of ornithology, that usually has to be reconstructed and tracked through dates and places depicted on the labels of specimens in ornithological collections. For instance, the ~35 years of collecting expertise of Bob Dickerman in Mexico and Central America have yielded more than 8,000 specimens, deposited in at least 16 museums in Canada, USA, and Mexico. Several have represented new taxa and, as a whole, they are one of the most complete avifaunal surveys developed by any bird collector in the region. Another interesting aspect is nostalgia. Anyone, anywhere in the world that is confronted with a series of memories of field workers, arrives at the point of environmental deterioration. Through the pages we get to places that are now long gone in a preserved state, and also learn about the evolution of road systems in Mexico and Central America, and the problematic security for developing field work in many regions at present. One also realizes that something has not changed at all: the hospitality of locals even in the most remote localities.

It is, however, not a simple book to read. After the first few chapters, and understanding that the Los Tuxtlas and Tamaulipas regions are most favored by researchers (given the close proximity to Mexico and the fact that some of the authors participated in the same expeditions), the narrations get to common places, and listings of taxa collected or observed become boring. Nevertheless, I really enjoyed the different ways the authors perceived the culture and the environment, and clear differences in perception arise between those that participated in one or a few collecting trips, and those that spent long periods in or moved to the region.

The major bias of this book is that it largely represents the "gringo visitor" point of view

(only one of the authors is Mexican while the others are North American or European), and therefore presents a situation in which U.S. researchers come to the tropics as leaders, teachers, or trainers, and local roles are those of field assistants and guides, leaving little room for true scientific collaboration among locals. This issue was true for several decades until the late 1970s and the book is really pitiful for not having writings by the late Bernardo Villa, Mario Ramos, and Allan Phillips (as noted by the Editor's Afterword). It should have included more representatives of recent generations of zoologists, especially locals, for which true scientific collaboration is the way to proceed in field work across a broad spectrum of activities that include collecting, measuring, recording, and censusing populations. However, this is not Kevin Winker's fault, given that several authors failed to submit collaborations. Also, common allusions to Dwain Warner's influence along the chapters is understandable, given that Winker belonged to that research group and authors associated with it were more prone to respond than others.

Some details might have improved the book. For example, photographs are scarce or absent in most of the chapters. Scientific names (apparently added by Winker) are at times misspelled and, at other times, erroneously assigned (e.g., *Sturnus* for Meadowlarks [*Sturnella*], or *Quiscalus major* assigned to Boat-tailed Grackles from Chiapas [indeed *Q. mexicanus*]). In spite of these minor issues, the book is worthwhile to read, and a must in natural history libraries, because it also represents a nice addition to the growing literature on the history of ornithology and biological exploration. Many readers will read it with nostalgia, others trying to recall unknown aspects of the Central American natural environment. The main audience must be the younger generation of field naturalists in the Neotropics, because among its pages, they will find experience, scholarship, and passion through the very words of those field workers that contributed (and some still do) to the development of Latin American science. I thank C. E. Braun for comments and help in improving the English.—ADOLFO G. NAVARRO-SIGÜENZA, Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70-399, México D. F. 04510, Mexico; e-mail: fcvg01@unam.mx

WYTHAM WOODS: OXFORD'S ECOLOGICAL LABORATORY. Edited by Peter S. Savill, Christopher M. Perrins, Keith J. Kirby, and Nigel Fisher. Oxford University Press, Oxford, UK. 2010: xvii + 263 pages, 80 illustrations, 8 pages of color plates. ISBN: 978-0-19-954320-5. $99.00 (cloth).—There isn't, or at least there shouldn't be, an ornithologist anywhere who would fail to recognize Wytham Woods as the site of possibly the single most productive study of avian populations ever conducted, that of Great (*Parus major*) and Eurasian Blue (*Cyanistes caeruleus*) tits, started in 1946 by John Gibb shortly after David Lack, the new Director of the nearby Edward Grey Institute (EGI), decided to give up studying European Robins (*Erithicus rubecula*) in favor of nest-box studies. However, this is but one of the many distinguished studies conducted in what is, as described by Chris Perrins in the Introduction to this volume, a "very ordinary...-piece of ash-maple-hazel woodland typical of central England" that's not even particularly large, being only about 1,250 ha (2,750 acres) in size compared to, say, Hubbard Brook in New Hampshire—perhaps the closest analogue to Wytham Woods in the U.S.—which is 3,160 ha (6,952 acres). Yet, as Montagu Bertie, the fifth Earl of Abingdon, might have commented after the Enclosure Act of 1814 allowed him to buy out the various small freeholders and consolidate most of what is now the Wytham Woods estate, "mighty oaks from little acorns grow"—and scientifically, at least, the area ranks among the mightiest plots of land on earth.

This fascinating book provides a history of Wytham Woods accessible to professionals and general readers alike, from its glaciated beginnings to recent controversies over land-use practices that eventually wrestled control of the estate from the Oxford University Forestry Department, whose management focused entirely on improving the quantity of timber production, to a committee representing the interests of the broader university, thus opening up the estate to a wide range of ecological investigations. And an impressive set of studies they are, many of which are succinctly summarized here in chapters written by key figures focusing on the trees, flowers, invertebrates, birds, and mammals as well as overall land use and conservation management. (I'm not sure why reptiles and amphibians were left out unless it's a reflection of a relative paucity of herpetologists in the U.K.).

Among the many eminent ecologists and evolutionary biologists who have done important work in Wytham Woods, besides Lack and Gibb, are Dennis Chitty, Nick Davies, Charles Elton, Paul Feeny, Mike Hassell, Alex Kacelnik, Bernard Kettlewell, John Krebs, Hans Kruuk, David Macdonald, Ian Newton, Chris Perrins, Mick Southern, Richard Southwood, and George Varley, an incomplete list that offers incontrovertible proof that one needn't necessarily conduct a study in some exotic locale to be internationally successful.

One of the reoccurring themes of this book is the immense value of long-term studies as a means of generating data that can be used to address new questions such as climate change as well as provide a fertile venue for applying new technologies like radio-tracking, passive integrated transponders, and molecular genetics, to name a few. In most cases, such studies are not conducted by a single individual, but rather by a series of students and researchers. Nowhere has this process been conducted more successfully than in Wytham Woods, where some 40 students have completed theses involving some aspect of the tit study alone, each contributing his or her piece to a study that has successfully defined the cutting edge of avian ecology for decades. Of course, facilitating this is the U.K. system of higher education, which gives a Ph.D. student 3 years, and only 3 years, to conduct original research and write a thesis—half the length of time it takes to get an ecology Ph.D. in the U.S. Yet the system clearly works, and even if the seemingly frenetic time schedule followed by Ph.D.s in the U.K. is unrealistic for most American students, the potential advantages of plugging into an established study, as demonstrated by the dozens of students who have successfully worked on the Wytham Wood tits, deserve to be more widely recognized by U.S. academics.

And still there remain much to be done. Interestingly, although the original idea of putting out nest boxes for birds came from foresters who were hoping to decrease losses to defoliating caterpillars by increasing tit populations, it's still unclear whether increasing tit densities reduces caterpillars or not. This and several other examples discussed in the book illustrate that the precise consequences of many, if not most, ecological interactions are at best uncertain. Apparently neither the American nor the British models of higher education are likely to put ecologists out of business any time soon! However, if we are ever to understand complex ecological interactions, surely key insights will come from places like Wytham Woods where there has been intense long-term study of multiple components of the ecosystem.

All ecologists will find much of interest in this book, whether they have spent time at Oxford and the EGI or not. For those of us who are farther along in our careers, the historical perspective provided by the book is fascinating. For those starting out, the book offers numerous examples of how workers at Wytham Woods have launched their own successful careers while taking advantage of the wealth of prior information provided by earlier generations of students. Particularly standing to benefit is anyone in a position to initiate or continue long-term studies, whether they be of trees or birds. Doing so can be difficult, both because of the problems of obtaining continuous funding and the difficulties of envisioning the value of work that may not be fully realized for 25, 50, or even 100 years—long after one has (hopefully) obtained whatever degrees one is going to get. But then, this is also long after most, if not all, of our published works will have outlived their usefulness, and what better legacy could any of us leave than data that can be followed up on by future generations of students, allowing them the means to answer questions which we have yet to even formulate?—WALTER D. KOENIG, Senior Scientist, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA; e-mail: wdk4@cornell.edu

ALL ABOUT BIRDS, A SHORT ILLUSTRATED HISTORY OF ORNITHOLOGY. By Valérie Chansigaud. Princeton University Press, Princeton, New Jersey, USA. 2010: 239 pages, many color and black-and-white illustrations. ISBN: 978-0-691-14519-8. $29.95 (hardcover).—This book was previously published in 2009 as "*The History of Ornithology*" in the United Kingdom by New Holland Publishers, when it was translated from French into English from its 2007 "*Histoire de l'ornithologie*", published in France by Delachaux & Niestlé.

Chapters are arranged by century with a focus on ornithology in Europe since the 1500s, and the text consists mainly of biographical sketches

of historically important ornithologists. The index lists 769 people, mainly ornithologists, but also illustrators and administrators. The bibliography cites nothing published by the ornithologists who are sketched in the book; instead, it cites only secondary sources, 14 for the history of ornithology, 16 for the history of illustration, and 11 for the history of natural history. A colored timeline at the end of the book summarizes the historical points of references, voyages and discoveries, the major events in ornithology by country, and the institutionalization of ornithology in museums and societies with an emphasis on France.

In comparison, a recent book by Michael Walters (2003) has an extensive bibliography, mainly of primary sources with 334 entries. The two books are about the same length (255 pages and more text per page in Walters). Both books draw on the comprehensive book by Stresemann (1951, 1975), which developed the history of ornithology from classical times through the first half of the past century. Both the Chansigaud and Walters books are arranged first by century and within century by country of the ornithologists. Chansigaud includes photographs of early ornithologists, whereas the corresponding photographs in Walters are larger, sharper, and with more contrast; apparently both books used the same image sources. Chansigaud includes images of period paintings and photographs of bird specimens as they were painted for the early monographs. The bibliographic sketches in Walters are more detailed and interesting to read, the deposition of their specimens in museums is reported, and the historical and social links between ornithologists are explored in Walters (2003) but generally not in Chansigaud (2010). For example, Walters describes the positive intellectual and institutional influence of Buffon on the early evolutionary ornithologist Lamarck and the brilliant and "most odious of men", Cuvier, who publicly humiliated the older Lamarck in Lamarck's own lecture room. Lamarck subsequently lost his students, who were his last source of financial support; his daughters then had to beg for food. When he died he "was buried in a pauper's grave", and Cuvier's obituary of Lamarck was so vicious that the Académie Française in publishing a memorial volume to Lamarck refused to publish Cuvier's contribution. Chansigaud does not develop the theme of influences and the give-and-take between the early ornithologists. In another example, Chansigaud's account on Hume and his work in India has more on Hume's substantial political and educational accomplishments than on his ornithological contributions. In contrast, Walters notes that Hume accumulated a collection of 63,000 bird skins and 19,000 eggs (now in the British Museum [Natural History]) and the largest ornithological library in Asia; Hume's manuscript book on the ornithology of India was never published because a servant sold the manuscript in the market as waste paper. Walters (2003) includes appendices of the systematic arrangements of birds from Charleton (1668) through Linnaeus, Brünnich, Latham, Pallas, Gloger, and others including Vieillot, Temminck, Bonaparte, Reichenow, and Fürbinger. These lists make fascinating material on the history of systematic ornithology, but this topic is not part of Chansigaud's book. The book ends with a mention of the important early molecular systematics work of Charles Sibley up to 1990.

Chansigaud includes many photographs of birds, both early black-and-white illustrations and more recent photographs of color plates and mounted specimens, each in its historical context; these illustrations are an important feature of the book. Another positive feature is the index of historically important ornithologists, and the biographic details are generally accurate. Both Chansigaud's and Walters's books include sections on the beginnings of American ornithology (Bartram, Wilson, Audubon, Bonaparte, Coues, Baird, and others in North America; Marcgraf, Don Felix d'Azara, von Spix, von Ihering, and Schomburgk through Hudson in South America); Chansigaud gives more attention to the development of birding. The history of ornithology in America also has been developed recently by Barrow (1998) and Weidensaul (2007) with their accounts limited to the ABA area of North America. For a look at early ornithology and ornithologists, the facts in the book appear generally accurate, but as is evident in the titles of the United Kingdom and French editions, *All About Birds* is a set of historical biographies and, as in the subtitle of this edition, is not all about birds.—ROBERT B. PAYNE, Professor Emeritus, University of Michigan, 1306 Granger Avenue, Ann Arbor, MI 48104, USA; e-mail: rbpayne@umich.edu

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INVISIBLE CONNECTIONS: WHY MIGRATING SHOREBIRDS NEED THE YELLOW SEA. By Peter Battley, Brian McCaffery, Danny Rogers, Jae-Sang Hong, Nial Moores, Ju Yung-Ki, Jan Lewis, and Theunis Piersma. Photographs by Jan van de Kam. CSIRO Publishing, Collingwood, Victoria, Australia. 2010: 160 pages, 240 photographs. ISBN: 978-0-643-09659-2. $49.95 AU (paper).—No other group of migratory birds is as perilously wedded to a relative handful of critical stopover sites as the shorebirds. Crisscrossing the globe, undertaking some of the longest nonstop migrations ever documented (including, in the case of the Bar-tailed Godwit [*Limosa lapponica*], *the* longest), shorebirds depend on abundant, concentrated food resources to fuel their hemispheric odysseys.

Few such stopover sites are as important as the Yellow Sea, through which most of the East Asian-Australasian flyway funnels every year. Millions of shorebirds commuting between Alaska, Siberia, central and south Asia, Indonesia, New Zealand, and Australia congregate on the sea's vast and fecund tidal flats. A third of all the flyway's shorebirds gather along the Yellow Sea each spring; for the godwits, among others, the entire flyway population concentrates there during migration. The importance of the Yellow Sea for such imperiled species as Nordmann's Greenshank (*Tringa guttifer*), or the Spoon-billed Sandpiper (*Eurynorhynchus pygmeus*)–the world's rarest shorebird–cannot be overstated.

The Yellow Sea is also home to 600 million people, many of whom, like the shorebirds, depend upon healthy shellfish populations for their livelihoods. But as this book lays out in words and images, both fishermen and birds face an uncertain future. South Korea in particular has embarked on a campaign of tidal "reclamation," resulting in the loss of hundreds of square kilometers of formerly rich foraging habitat. The infamous Saemangeum Project alone has impacted 400 km^2 of formerly prime shorebird habitat.

Invisible Connections is a beautifully illustrated plea on behalf of birds whose lives are linked to the health of the Yellow Sea ecosystem, and whose migrations encompass more than half the globe. Written by seven noted shorebird biologists from the U.S., South Korea, Australia, New Zealand, and the Netherlands, the meaty text is almost secondary to the stunning images of Dutch photographer Jan van de Kam, whose obsession with shorebirds pays glorious dividends here. The combination is an eloquent argument for preserving this migratory phenomenon.

Van de Kam's photographs are arrestingly beautiful. Following the migrants from their tundra breeding areas in Siberia and Alaska, to such starkly lovely sites as Roebuck Bay in northwest Australia, where he captures greenshanks and kangaroos in the same frame, van de Kam shows the full sweep of the East Asian-Australasian flyway. His images are rich in shorebird behavior, but most striking are those–especially photographs taken on the Yellow Sea–that show the profound impact of humans on shorebird habitat, and the linked fortunes of people, especially shell fishermen, and birds. (Among the more fascinating are a series of photos of former shorebird hunters near Shanghai who now use traditional tools like decoys and bamboo whistles to trap migrant shorebirds in clap nets for scientists, instead of for the pot.).

This is an English-only version of an originally trilingual (English, Chinese, and Korean) edition first published in 2008 by Wetlands International to mark the Ramsar Conference in South Korea. Like its predecessor, this book is meant to capture the eye and sympathies of the general public, a task for which it is well-suited. The photographs are the obvious hook for non-specialists, but the text is engagingly written and does an excellent job of conveying both the immense drama of the trans/circum-Pacific migration, and the critical nature of the Yellow Sea to its migrants.

The opening chapter, by Alaskan biologist Brian McCaffery, sums up the volume's theme:

"Time is Running Out." Subsequent chapters include "Shorebird Lifestyles," "Flyways," "The Tundra," "A Southern Holiday?," "Tidal Flat Specialists," and "International Partnerships." Nial Moores, founder of Birds Korea, and South Korean conservationist Ju Yung-Ki, end the book with "The Heart of the Flyway," directly discussing the threats and opportunities in the Yellow Sea region.

I have just one criticism. For a book at whose heart lies geography, the general absence of maps (except for a few small ones that show overall flyway patterns), is puzzling and unfortunate. Most strangely, there is no map of the Yellow Sea itself, leaving those unfamiliar with the region at a loss to easily locate the many sites mentioned in the text and captions. This single failing aside, *Invisible Connections* is a gem–and conservationists everywhere can only hope it has the desired effect.—SCOTT WEIDENSAUL, 778 Schwartz Valley Road, Schuylkill Haven, PA 17972, USA; e-mail: scottweidensaul@verizon.net

A PHOTOGRAPHIC GUIDE TO THE BIRDS OF JAMAICA. By Ann Haynes-Sutton, Audrey Downer, Robert Sutton, and Yves-Jacques Rey-Millet. Princeton University Press, Princeton, New Jersey, USA. 2010: 304 pages, 6 figures, 650 color photographs, and 220 maps. ISBN: 978-0-691-14391-0. $29.95 (paper).—Peter Vogel and Catherine Levy asserted that "Conservation of habitat is the primary measure that will save the birds of Jamaica...Most non-government organizations are lacking the financial and human resources to carry out the work that is necessary, such as advocacy addressed to the government and decision makers" (Raffaele et al. 1998:30, *A Guide to the Birds of the West Indies*, Princeton University Press, Princeton, NJ, USA). These words seem particularly prescient today, as the Jamaican government is poised to sell the Font Hill Nature Preserve, an extraordinary stand of old-growth mangroves (especially black mangrove, *Avicennia germinans*), ponds, and beaches, for an 800-unit resort hotel (full disclosure: I've worked there since 1986). Field guides can't by themselves protect threatened habitats, widespread in Jamaica, but do comprise an important tool to educate people able to influence decision makers.

The new *Photographic Guide to the Birds of Jamaica* is the first book to occupy the niche of comprehensive bird guide for Jamaica. It's beautifully produced, compact (127 × 190 mm [5″ × 7.5″]), and durably bound, using semi-gloss paper in an easy-to-use format with typically a page per species, or two pages in the case of most endemics. Rey-Millet treats us to gorgeous photographs—up to five per species, some filling the page—typically single-flash, and perfectly exposed. The multiple photographs accompanying many accounts highlight variation in posture, vantages on plumage, and age/male or female.

A comprehensive, stand-alone Jamaican field guide will benefit Jamaicans in particular, and is long overdue considering the island's species richness and endemism: 307 bird species—127 breeding and 180 regular migrants. Forty-eight species (> 15% of the avifauna) are either endemic species or subspecies, or Caribbean endemics. Jamaica has more endemic bird species—vividly described in the first chapter of Roland H. Wauer's *A Birder's West Indies: an Island-by-Island Tour* (1996, University of Texas Press, Austin, USA)—than any other Caribbean island including much larger Cuba and, for reasons not entirely understood, but probably linked to the Caribbean region's complex geological history. Jamaica has its own tody (*Todus todus*), and four endemic genera: *Trochilus* (two streamertail hummingbird species), *Loxipasser anoxanthus* (Yellow-shouldered Grassquit), *Euneornis campestris* (Orangequit), and *Nesopsar nigerrimus* (Jamaican Blackbird). Several taxa challenge birdwatchers, including 23 sandpipers, 25 wood warblers, 12 pigeons/doves, and eight tyrannid flycatchers.

This new photographic field guide is organized into an Introduction (19 pages), and sections on "Birding in Jamaica" (8 pages), "How to use this book" (3 pages), and species accounts (236 pages). The introduction covers Jamaica's location, climate, geology and geomorphology, topography, and habitats (12 pages); composition and origins of the avifauna; bird movements including winter, austral, and elevational migrations; conservation issues and threats, reinforcing the importance of habitat and invasive species; and a history of Jamaican ornithology including bibliography. The birding section briefly describes and maps 16 locations with distinctive habitats (including photographs) and species. This birding section also provides useful information for birders, such as trip tips, issues of security,

hazards, and—usefully—the lead author's e-mail address.

The species accounts are standardized for quick reference to all species names, taxonomy (e.g., monotypic, polytypic), body length, plumage descriptions, similar species, voice, and habitat and behavior—foraging, diet, and nesting. Each account also contains a boxed description of geographic range and status in Jamaica (e.g., endemic, resident, winter visitor, transient; and abundance category); standard country map, color-coded and contoured for up to two levels of abundance/reliability of occurrence; and relevant IUCN redlist category (critically endangered, endangered, vulnerable, near threatened).

Seven helpful appendices include "Probably extinct species" (up to 6 in total, 3 illustrated, but not the 2 macaws and a parrot), "Vagrants" (77 of the total 307 species listed with plumage descriptions), "Species endemic to Jamaica" (30 species), "Subspecies endemic to Jamaica" (19 species), "Caribbean endemic species and subspecies recorded in Jamaica" (18 species), and a list of species with commercially available vocalizations. The index includes just Latin binomial and English common species names, and a quick index inside the back cover includes 65 of the primary bird groups, mostly families. I found just a handful of errors, mostly typographic, but Colombia was misspelled.

Haynes-Sutton and Rey-Millet intended and accomplished, in collaboration with Downer and Sutton (neither of whom, sadly, lived to enjoy the finished product), a major improvement on Downer's and Sutton's 1990 edition (*Birds of Jamaica—A Photographic Field Guide*, Cambridge University Press, Cambridge, UK). The new guide most importantly includes photos of all Jamaican species except the vagrants: 627 bird photos of 219 species, compared to just 64 bird photos of 47 species, emphasizing endemics, in the Downer and Sutton edition. The new book also includes or expands "habitats and behavior" sections for all photographed species.

Several Caribbean field guides benefit from regional comprehensiveness, but at the expense of local detail. Most notable for decades was James Bond's *Birds of the West Indies* (on my bookshelf the 5th Edition, 1993, Houghton Mifflin Company, Boston, MA, USA). A guide of the same title was published by Helm in 1998, and by Harper Collins in a new 2010 edition, with standard-format illustrations of 632 species—including visitors and vagrants, and all residents except for Trinidad and Tobago—but lacking illustrations of racial variation among islands, and with short species accounts. Two linked guides are also valuable: Raffaele et al. (1998) presents excellent accounts of all species including migrants, at the costs of bulkiness for a field guide and separation of species plates from accounts. Raffaele et al. (2003, *Princeton Field Guides: Birds of the West Indies*, Princeton University Press, Princeton, NJ, USA) subsequently produced an efficient field guide by shortening species accounts, located on opposite pages to illustrations, in a smaller, durable package. The latter two guides facilitate comparisons by grouping similar species on plates (basically the same plates, except for some larger format, single-species illustrations in the 1998 guide). The new Jamaican guide best captures the birds' vivid colors, and lavishes more attention on Jamaica's birds by focusing geographically, including mapped species distributions *within* the island and more detailed species accounts in some cases. For example, more information is available to distinguish Sad from Stolid flycatchers (*Myiarchus barbirostris*, and *M. stolidus*, respectively), and I learned that the Orangequit ranges to sea level only on Jamaica's wetter northeast coast. No electronic app (e.g., for iPhone) is yet available for Jamaican birds as for *Birds of Dominican Republic and Haiti* (http://press.princeton.edu/blog/2010/06/02/the-birds-of-the-dominican-republic-and-haiti-iphone-app-available-all-proceeds-go-to-disaster-relief/).

This new photographic guide will facilitate identifying and appreciating all regularly encountered Jamaican birds. The more we, and especially Jamaicans, come to know the island's avifauna the better, since environmental threats are here to stay.—THOMAS W. SHERRY, Professor, Department of Ecology and Evolutionary Biology, 400 Boggs Hall, Tulane University, New Orleans, LA 70118, USA; e-mail: tsherry@tulane.edu

DO HUMMINGBIRDS HUM? FASCINATING ANSWERS TO QUESTIONS ABOUT HUMMINGBIRDS. By George C. West and Carol A. Butler. Rutgers University Press, Piscataway, New Jersey, USA. 2010: 185 pages, 32 figures, and 8 color plates. ISBN: 978-0-8135-4738-1. $21.95 (paper).—This book contains 87 questions about hummingbirds organized into

nine chapters, plus four appendices and an extensive reference section. Hummingbirds are the favorites of many birders, casual observers, gardeners, homeowners, and ornithologists piquing curiosity with their extreme lifestyles and biology, tiny size, bright colors, and engaging behaviors.

George West and Carol Butler have teamed up to produce this fourth in the Rutgers Animal Q&A Series. Butler authored the three previous titles in this series. West is a Professor Emeritus of Zoophysiology at the University of Alaska, Fairbanks, and a researcher on the physiology and ecology of birds. He has published more than one hundred scientific papers, provided hundreds of illustrations for others, and recently published the revised and updated *A Birder's Guide to Alaska*.

The book is organized into nine main chapters: Hummingbird Basics, Systems and Senses, Feathers and Bones, Reproduction, Flight and Migration, Dangers and Defenses, Attracting and Feeding, Identifying and Photographing, and Research and Conservation. There are four appendices covering hummingbird garden plants, places to see hummingbirds, hummingbird organizations, and recommended reading and web sites. A useful feature is the References section, which follows the organization of the book and provides the literature support for many of the answers. This particular section might have been made easier to use by boldfacing the chapter titles, as the questions in each of the nine chapters restart numbering again from 1. Thus, there are as many as nine questions with the same number in this section.

As a reviewer, I read the book sequentially, but the format allows, and is intended for, readers to simply look up a topic for which they seek an answer. The answers are thorough and well researched, but they are also self-contained for the most part even when a topic is complex, using repetition of material to facilitate as clear an understanding as possible by reading only the answer to the relevant question. There are internal references to other answers for more complex topics. As a hummingbird researcher who gives frequent public programs, I get asked a lot of questions, and it appears that virtually every possible question about hummingbirds has been included in this book. Obvious questions like "How many species of hummingbirds are there in the world?" and "Where is the best place to hang my hummingbird feeder?" to less typical ones like "When do hummingbirds molt?" and, of course, the question that titles the book, are covered with equal depth and comprehensiveness.

As an Eastern birder, I do notice a western flavor to many of the answers, but given that the majority of U.S. species are western this makes perfect sense. In a few instances, exceptions that the eastern Ruby-throated Hummingbird (*Archilochus colubris*) presents are overlooked, including for example the role that insects may have in their diet for fat deposition prior to migration. One minor quibble is that my personal favorite bird name, Rainbow Starfrontlet (*Coeligena iris*), did not make the list of "Descriptive Hummingbird Names".

Few actual errors are evident. The most immediately apparent is the top photograph on color plate F, which is captioned as a Chestnut-breasted Coronet (*Boissonneaua matthewsii*) but is clearly not that species, but rather is a Shining Sunbeam (*Aglaeactis cupripennis*). Another error appears in Figure 23, where breeding and winter ranges, and migration routes, are shown for both Rufous Hummingbird (*Selasphorus rufus*) and Ruby-throated Hummingbird. There is a migration arrow for Ruby-throated from the Yucatan of Mexico to the Florida Peninsula. Robinson et al. (1996, *The Birds of North America. Number 204.*) do not depict this migration route, and the species is extremely scarce anywhere in the Caribbean. These few minor issues and errors could easily be remedied in a second printing but, regardless, I highly recommend this book for anyone who has an interest in hummingbirds, or interacts with the public about birds in any way.—ALLEN T. CHARTIER, 1442 West River Park Drive, Inkster, MI 48141, USA; e-mail: amazilia1@comcast.net

The Wilson Journal of Ornithology 122(4):820–832, 2010

PROCEEDINGS OF THE NINETY-FIRST ANNUAL MEETING

JOHN A. SMALLWOOD, SECRETARY

The Ninety-first Annual Meeting of the Wilson Ornithological Society was held from Thursday, 20 May, through Sunday, 23 May 2010, on the campus of Hobart and William Smith Colleges in Geneva, New York. Mark E. Deutschlander, Chair of the Biology Department at Hobart and William Smith (HWS) Colleges, chaired the Local Committee, which also included Kristi Hannam of SUNY Geneseo, Sara Morris of Canisius College, Margaret Voss of Behrend College at Penn State Erie, John Waud of the Rochester Institute of Technology, Erica Cooney-Connor and Nancy Wilde of HWS Conference and Events, and Pat Heieck of HWS Dining Services.

The Council met from 0900 to 1600 hrs on Thursday, 20 May, at the Finger Lakes Institute on the HWS campus. That evening there was an ice-breaker social for conferees and guests at the HWS Scandling Center.

The opening session on Friday convened in the Albright Auditorium at 0841 hrs with welcoming remarks from Mark E. Deutschlander, WOS President E. Dale Kennedy, and WOS Second Vice-President and Chair of the Scientific Program Committee, Robert L. Curry. After presenting several items of information for the conferees, Vice-President Curry concluded the opening ceremony by introducing Edward H. Burtt Jr., who in turn introduced the Margaret Morse Nice Lecture and the plenary speakers, Robert B. Payne and Laura Payne, who delivered an informative presentation, "Brood parasitism in cuckoos, cowbirds, and African finches."

The scientific program included 44 papers organized into 10 sessions, 30 posters, and two symposia consisting of six papers on migratory physiology and energetics, and six papers on the effects of energy development on birds. At the conclusion of oral presentations on Friday afternoon, the conferees were treated to a screening of a remarkable documentary film on the search for Ivory-billed Woodpeckers (*Campephilus principalis*) near the town of Brinkley, Arkansas. The evening concluded with a reception in the Vandervort Room of the Scandling Center, which coincided with the poster session.

The Local Committee hosted birding forays in the vicinity of the conference site each day from Thursday through Sunday. In addition, longer trips were scheduled for Thursday to the Cornell Laboratory of Ornithology; for Friday and Saturday, on a tour of the Finger Lakes Region known as the Ontario Pathways; and on Sunday, to the Montezuma Wetlands Complex.

The conferees enjoyed a social hour prior to the annual banquet, which also was held in the Vandervort Room. The evening events included an enjoyable dinner, and afterwards WOS President E. Dale Kennedy joined those assembled in thanks to the many persons whose hard work had resulted in a successful conference. President Kennedy also thanked the three elected members of Council who had completed their terms of office, Robert S. Mulvihill, Timothy J. O'Connell, and Mia R. Revels, and welcomed the three newly elected members of Council, Mark E. Deutschlander, Paul G. Rodewald, and Rebecca J. Safran. The following WOS awards and commendations also were presented:

MARGARET MORSE NICE MEDAL

(for the WOS plenary lecture)

Robert B. Payne and Laura Payne, "Brood parasitism in cuckoos, cowbirds, and African finches."

EDWARD'S PRIZE

(for the best major article in volume 121 of *The Wilson Journal of Ornithology*)

W. Andrew Cox and Thomas E. Martin, "Breeding biology of the Three-striped Warbler in Venezuela: a contrast between tropical and temperate parulids."

STORRS L. OLSON PRIZE

(for the best book review in volume 121 of *The Wilson Journal of Ornithology*.)

Richard C. Banks, "The white-cheeked geese: *Branta canadensis*, *B. maxima*, *B.* "*lawrensis*", *B. hutchinsii*, *B. leucopareia*, and *B. minima*. Ecophysiographic relationships, biogeography, and evolutionary considerations. Volume 2. Western taxa, biogeography, and evolutionary considerations."

WILLIAM AND NANCY KLAMM SERVICE AWARD
(for distinguished service to the Wilson Ornithological Society)

Jerome A. Jackson.

LOUIS AGASSIZ FUERTES AWARDS

Jessica Oswald, University of Florida, "The biogeography of birds in Peruvian tropical dry forests."

Christopher Tonra, University of Maine, "Determining the relative influence of environmental and endogenous factors on the transition from nonbreeding to breeding in migratory songbirds."

GEORGE A. HALL/HAROLD F. MAYFIELD AWARD

Nanette Mickle, of Woodbridge, Virginia, "Tracking long-distant songbird migration (Purple Martins) using geo-locators."

PAUL A. STEWART AWARDS

Allison Cox, University of Missouri, "Natal dispersal of Red-bellied Woodpeckers in a fragmented landscape."

Kira Delmore, University of British Columbia, "Divergent migratory behaviors as post-zygotic barriers to interbreeding in hybrid zones."

Luke Powell, Louisiana State University, "Using home range estimates and 30 years of mist-net captures to determine the effect of land use history on dispersal of Amazonian birds."

Barry Robinson, University of Alberta, "Arctic Peregrine Falcons as indicators of trophic dynamics in coastal ecosystems."

Taza Schaming, Cornell University, "The impact of whitebark pine mortality on Clark's Nutcracker demography and habitat use."

Daphna Shaw, University of Florida, "Male parental investment, relatedness, population density, and territorial proximity as factors promoting extra-pair paternity in the Northern Mockingbird."

Deborah Visco, Tulane University, "Ontogenetic mortality rates in a neotropical understory passerine."

Kara-Anne Ward, University of Windsor, "Female mate search tactics in Long-tailed Manakins: a novel tracking system for monitoring social interactions."

ALEXANDER WILSON PRIZE
(for best student paper)

Stephanie G. Wright, Villanova University, "Hybrid chickadee vocalizations change as the hybrid zone moves northward in southeastern Pennsylvania."

LYNDS JONES PRIZE
(for best student poster presentation)

Jason M. Townsend, SUNY-College of Environmental Science and Forestry, "Mercury bioaccumulation in *Catharus* thrushes along an elevational gradient."

NANCY KLAMM BEST UNDERGRADUATE STUDENT ORAL PAPER AWARD

Christina Masco, Cornell University, "Individuality and recognition in the Great Black-backed Gull, *Larus marinus*."

NANCY KLAMM BEST UNDERGRADUATE STUDENT POSTER AWARD
(Their posters judged a tie, two students share this year's award.)

Anne Lugg, Kutztown University, "Aging House Wren nestlings based on feather tract development, wing chord, and head length."

Jordan S. Kalish, Ohio Wesleyan University, "Bacteria and fungi in the plumage of birds of prey."

WILSON ORNITHOLOGICAL SOCIETY TRAVEL AWARDS

Aubrey Alamshah, Ohio Wesleyan University, "Seasonal changes in maintenance behavior of the House Sparrow (*Passer domesticus*)."

Katie Clower, University of Minnesota, "The effects of rotational grazing on relative abundance of grassland songbirds."

James Garabedian, Frostburg State University, "Habitat associations of over-wintering birds in restored hayfields in the Manassas National Battlefield Park, Virginia."

Jessie Hoguc-Morgenstern, Denison University, "The relationship of migrant avian frugivory and honeysuckle (*Lonicera*) management in the fall."

Gustavo Londoño, University of Florida, "Breeding biology of five species of high elevation Andean tanagers."

Lawrence Long, The Ohio State University, "Survey of Lake Erie island passerine nest predation."

Anne Lugg, Kutztown University, "Aging House Wren nestlings based on feather tract development, wing chord, and head length."

Adrian Monroe, Oklahoma State University,

"Winter bird response to heterogeneity-based management in a tallgrass prairie."

Erica Mueller, Montclair State University, "A spectrographic analysis of American Kestrel (*Falco sparverius*) vocalizations. Do broodmates sound more like each other than non-related broods?"

Benjamin Padilla, Gordon College, "The effects of natural and human induced edges on foraging flocks of wintering songbirds in southern New England."

Monika Parsons, University of Maine, "Quantifying incubation behavior of Common Eiders nesting on Jordan's Delight Island, Maine."

Ashley Rathman, Kutztown University, "The effect of Wood Thrush hosts on the survival of Brown-headed Cowbird eggs and nestlings."

Sonya Richmond, University of Toronto, "Influence of adult age on Rose-breasted Grosbeak nestling provisioning rates in stands harvested by single-tree selection."

Marla Steele, Oklahoma State University, "Effects of cold front passage on migrant raptors at Shirakaba Pass, Nagano Prefecture, Japan, autumn 2000–2009."

Brynne Stumpe, Canisius College, "The effects of a residential wind turbine on bird behavior."

Emily Thomas, Penn State University, "Effects of oil and gas development on songbirds."

Judit Ungvari-Martin, University of Florida, "Variation in understory forest bird communities of Amazonian forests on different soils."

Gretchen Wagner, CUNY Hunter College, "Patterns of Brown-headed Cowbird parasitism on Eastern Phoebes: a ten-year comparison."

Whitney Wiest, University of Delaware, "Development of a bird community integrity index to monitor salt marsh condition at national wildlife refuges."

Marie Wilson, University of the South, "The effects of exurbanization on the food and habitat of Pileated Woodpeckers (*Dryocopus pileatus*)."

Stephanie Wright, Villanova University, "Hybrid chickadee vocalizations change as the hybrid zone moves northward in southeastern Pennsylvania."

Selection committee for the Nice Medal: James D. Rising (Chair), Robert C. Beason, Robert L. Curry, Jerome A. Jackson, E. Dale Kennedy, Sara R. Morris; for the Edwards Prize: Clait E. Braun (Chair), James A. Cox, and Kevin Winker; for the Olson Prize: Clait E. Braun (Chair), and Storrs L. Olson; for the Klamm Service Award: Sara R. Morris (Chair), Richard C. Banks, Robert C. Beason, Robert L. Curry, and E. Dale Kennedy; for the Fuertes, Hall/Mayfield, and Stewart Awards: Carla J. Dove (Chair), John Bates, Terry Chesser, Greg Farley, Rob Faucett, Russ Greenberg, James Hare, Rebecca Holberton, Tom Jensen, E. Dale Kennedy, Sarah Kingston, Kevin McCracken, Chris Milensky, Patricia Escalante Pliego, Shane Pruett, Nate Rice, Scott Robinson, B. A. Schreiber, Sarah Sonsthagen, John Swaddle, Keith Tarvin, Pepper Trail, Jeff Walters, James Whatton, Chris Witt, Margaret A. Voss, and Douglas W. White; for the Alexander Wilson Prize, the Lynds Jones Prize, and the Nancy Klamm undergraduate presentation awards: Robert C. Beason (Chair), Edward H. Burtt Jr., John C. Kricher, Sara R. Morris, Mia R. Revels, John A. Smallwood, Margaret A. Voss, Doris J. Watt, and Douglas W. White; and for the WOS Travel Awards: Timothy J. O'Connell (Chair), Greg Keller, and Mia R. Revels.

COMMENDATION

WHEREAS THE WILSON ORNITHOLOGICAL SOCIETY held its annual meeting in Geneva, New York, on the campus of Hobart and William Smith Colleges, overlooking the stunningly beautiful Seneca Lake, and

RECOGNIZING that the Committee on the Scientific Program, under the adroit direction of Robert L. Curry, assisted by Robert C. Beason, Susan B. Smith, and Scott H. Stoleson, arranged and executed an exemplary exposition of oral and poster presentations, which included symposia exploring the physiology and energetics of migratory birds, and the effects of energy development on birds, and

RECOGNIZING that the Committee on Local Arrangements, through the efforts of Kristi Hannam, Sara Morris, Margaret Voss, John Waud, Erica Cooney-Conner, Nancy Wilde, and Pat Heieck, and particularly Chairperson Mark Deutschlander, who answered every request with a "yes" and whose many able assistants made those events come to pass, provided an excellent conference venue in a comfortable and welcoming campus environment in which dining experiences exceeded expectations, and

WHEREAS the conferees found this meeting both informative and enjoyable,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society commends the Committee on the Scientific Program, the Com-

mittee on Local Arrangements, and Hobart and William Smith Colleges for a most successful and rewarding meeting in Geneva.

BUSINESS MEETING

President E. Dale Kennedy called the annual business meeting to order at 1136 hrs, Friday, 21 May 2010 in the Geneva Room of the Warren Hunting Smith Library on the campus of Hobart and William Smith Colleges, Geneva, New York. Noting that a quorum was present, she introduced Secretary John A. Smallwood, who presented a synopsis of the Council meeting, which had taken place the previous day. As of 30 April 2010, the society's membership stood at 1,579 individuals, including 209 students, 216 international members, and 128 new members of all membership categories. While the renewal cycle was still underway, at that time the retention rate was 89%. In addition, 250 libraries and institutions subscribed to *The Wilson Journal of Ornithology*. Secretary Smallwood then asked those assembled to stand in recognition of the following members who were recently deceased: William A. Burnham and Carl D. Marti, both of Boise, ID.

Secretary Smallwood reported the society is in very good financial state with a healthy endowment of ~$2,500,000, and noted the value of these investments was increasing as the economy improves. On behalf of Council, the Secretary offered sincere gratitude to the WOS Finance, Audit, and Investment Committee, chaired by Allan Keith, for its astute management of societal assets.

Secretary Smallwood further reported that the Membership Committee, chaired by Timothy J. O'Connell, had revised and updated the WOS membership recruitment poster. Noting that the poster was currently on display, the Secretary invited those assembled to "check it out," to join the society and, if already a member, to encourage nonmember colleagues to join.

It was the Secretary's pleasure to report that Council had unanimously re-elected Clait E. Braun as Editor of *The Wilson Journal of Ornithology*, and he congratulated Editor Braun for doing a superb job, noting the *Journal* had grown to nearly a thousand pages, the quality is first rate, and his record for collecting page charges from authors has been outstanding.

Finally Secretary Smallwood announced that Council had proposed two changes to the Bylaws. First, under Article III, Section and Section 6, Council proposed to delete the sentences that require the President and the Treasurer to hold specific positions relative to OSNA. Second, Council proposed that the references to the society's journal be changed from the former name, *The Wilson Bulletin*, to the current name, *The Wilson Journal of Ornithology*. These proposed changes to the Bylaws will be voted upon by the membership at the next annual meeting, in Kearney, Nebraska, March 2011.

Secretary Smallwood then gave the floor back to President Kennedy, who summarized the Treasurer's report in the absence of the Treasurer (Melinda M. Clark), and introduced Editor Braun, who summarized the Editor's report. The written reports of the Treasurer and the Editor are included below.

Sara R. Morris, Chair, presented the report of the Nominating Committee, which also included Robert C. Beason, Mary Bomberger Brown, and Jameson Chase: President, E. Dale Kennedy; First Vice-President, Robert C. Beason; Second Vice-President, Robert L. Curry; Secretary, John A. Smallwood; Treasurer, Melinda M. Clark; Members of Council for 2010–2013 (three nominees for three positions), Mark E. Deutschlander, Paul G. Rodewald, and Rebecca J. Safran. Having asked for additional nominations from the floor and hearing none, President Kennedy closed the nominations as a result of a motion by Robert L. Curry, seconded by Jerome A. Jackson, which was unanimously passed by voice vote. Further, Timothy J. O'Connell moved and Jerome A. Jackson seconded that the Secretary cast a single unanimous vote for the slate of nominees. By acclamation it became so.

Second Vice-President Curry updated those assembled on the 2011 meeting, which will be a joint meeting with the Association of Field Ornithologists and the Cooper Ornithological Society, and will occur 9 to 13 March, in Kearney, Nebraska. Mary Bomberger Brown is serving as the local host. Vice-President Curry also announced that preparations were underway for the 2012 meeting: the WOS will be participating in the North American Ornithological Conference in Vancouver, British Columbia, 14–18 August. This meeting will take place on the campus of the University of British Columbia, and Kathy Martin will serve as the local chair.

Having completed the business at hand, President Kennedy inquired if any one present had additional items of business. Because no one did, Jed Burtt moved and Ted Davis seconded that we adjourn. This came to pass at 1204 hrs.

REPORT OF THE TREASURER

Statements of Revenues and Expenses for the Year Ending 31 December 2009

	2009 12 Months Actual	2009 Annual Budget	2010 Annual Budget
Revenues			
Contributions	$ 1,240	$ 1,800	$ 1,800
Student Travel Research Fund	720	300	500
Van Tyne Library Book Fund	212	100	110
Sales - back issues	282	240	200
Sales - books - Van Tyne Library	593	600	750
Subscriptions	13,065	15,100	12,000
Page charges	40,045	18,400	34,000
Royalties	7,837	4,230	1,000
BioOne Electronic Licensing	23,557	17,000	22,500
Mailing list rental income	85	222	270
Memberships	56,277	37,000	26,000
Other income	3,894	3,500	
Total revenues from operations	**$ 147,807**	**$ 98,492**	**$ 99,130**
Expenses			
Journal publication costs:			
Editorial honorarium	$ 4,000	$ 4,000	$ 6,000
Editor travel	982	1,700	1,350
Editor supplies/Mailings	2,768	1,700	2,620
Editorial assistance	21,123	24,000	18,500
Copyright expense	-	100	-
Printing - Journal	88,637	100,000	90,000
Artwork	750	1,000	750
Printing color plates	3,428	3,600	3,500
	$ 121,688	$ 136,100	$ 122,720
Operating expenses:			
Postage & mailing - back issues	$ 0	$ 440	$ 0
Storage back issues	-	350	240
Van Tyne Library - expenses	726	1,000	1,200
OSNA management services	14,193	24,300	16,000
Credit card fees	3,730	2,200	2,100
Travel expenses-OSNA rep	-	1,500	500
Travel expenses - general and Treasurer	370	800	1,000
Travel expenses-Ornith Council	-	300	250
Meeting expenses	100	3,750	3,000
Membership expenses	-	2,000	2,000
Accounting fees	4,165	4,500	4,000
Insurance - D&O	1,500	1,650	1,475
Office supplies	-	500	305
Postage - general	-	200	200
Other expenses	-	160	100
Filing fees	10	5	10
Discretionary expenses	-	3,000	3,000
	$ 24,794	$ 46,655	$ 35,380
Awards			
Student banquet	$ 2,415	$ 1,200	$ 1,200
Membership awards	-	600	600
Hall/Mayfield	1,000	1,000	1,000
Stewart	2,000	3,000	4,000
Fuertes	2,500	2,500	5,000
Klamm Service Award		2,000	1,000
Wilson, Lynds Jones, Klamm	700	700	700
Student travel grants	4,700	9,000	5,000

Award expenses	1,739	3,000	2,553
	$ 15,054	$ 21,800	$ 19,853
Contributions			
Support - Ornith Council	$ 9,300	$ 9,300	$ 15,000
Support - Ornith Council, restricted to revision costs	-	-	-
Am Bird Conservancy Dues		-	-
AAZN dues		250	250
	$ 9,300	$ 9,550	$ 15,250
Total Expenses	**$ 170,836**	**$ 214,105**	**$ 193,203**
Expenses in excess of revenues before investment income	**$ (23,029)**	**$ (115,613)**	**$ (94,073)**
Investment activity			
Revenues			
Investment earnings - budgeted	$ 0	$ 0	$ 0
Realized gain/loss - ML	(14,008)	35,000	27,081
Realized gains/losses-Howland	(47,404)	40,000	(20,000)
Realized gains/losses - Sutton	(3,033)	5,300	(2,000)
Unrealized gain/loss - ML	216,075	21,000	(150,000)
Unrealized gain/loss - Howland	143,664	5,000	(200,000)
Unrealized gain/loss - Sutton	15,416	9,800	(40,000)
Investment earnings - ML	23,411	27,000	41,760
Investment earnings - Howland	30,241	63,000	32,695
Investment earnings - Sutton	4,217	3,900	3,673
Total revenues from investment activity	$ 368,579	**$ 210,000**	**$ (306,791)**
Investment fees	**$ 19,240**	**$ 28,500**	**$ 14,366**
Investment revenues in excess of expenses	**$ 349,339**	**$ 181,500**	**$ (321,157)**
Total revenues in excess of expenses	**$ 326,310**	**$ 65,887**	**$ (415,230)**

STATEMENT OF FINANCIAL POSITION

31 December 2009

Assets	
Cash Investments:	
Merrill Lynch - cash	$ 150,452
Coamerica - Van Tyne checking	452
Van Tyne Univ. Michigan account	1,050
Sutton Fund - cash equivalents	28,164
Howland Mgmt - cash equivalent	193,342
Total cash and cash equivalents	$ 373,460
Other Investments:	
Merrill Lynch - common stocks	$ 595,227
Merrill Lynch - corp bonds	33,043
Merrill Lynch - mutual funds	37,155
Sutton Fund - equities	112,950
Sutton Fund - corp bonds	9,676
Howland Mgmt - equities	1,180,604
Howland Mgmt - fixed income	114,858
Total Other Investments	$ 2,083,513
Total Assets	$ 2,456,973
FUND BALANCES	
Fund Balances	
Restricted funds - Sutton Fund	$ 150,790
Unrestricted funds	491,069
Net Income	326,310
Fund balance - Klamm	$ 1,488,804
Total Fund Balances	$ 2,456,973

Melinda M. Clark, *Treasurer*

EDITOR'S REPORT

We received 206 new manuscripts in 2009 and published 124 dating from 2004 (1), 2005 (3), 2007 (21), 2008 (85), and 2009 (14) with a total published page count of 914. This included 28 Book Reviews, 1 Memorial, 1 Service Award, Proceedings of the Ninetieth Annual Meeting, List of Reviewers, Index, and the Table of Contents for Volume 121. Most papers published were from North America north of Mexico but the published material included 33 studies from 16 counties from outside of this area. Fifteen were from South America (Argentina = 4, Bolivia = 1, Brazil = 3, Chile = 1, Colombia = 1, Peru = 4, Venezuela = 1), 12 were from Central America (Costa Rica = 4, Ecuador = 4, Mexico = 3, Panama = 1), and the remainder were from other countries (Canary Islands and Spain = 2, China = 1, India = 2, Israel = 1). Over half of all manuscripts received in a specific year are rejected, withdrawn, or encouraged elsewhere in the initial year of receipt. Others may linger and eventually be withdrawn by the authors or the Editor for failure of authors to respond.

Electronic submission of all manuscripts is now encouraged effective as of 1 March 2010. We earlier encouraged electronic submission from authors outside of North America. All reviewers are contacted electronically and a few still request and return paper copy. Presently, we return paper copy to authors of first reviews and marked manuscripts, as it is still easier to protect reviewer confidentiality and to provide personal edits of manuscripts by paper copy. All subsequent correspondence and edits are done electronically. This process has some lingering issues (extremely slow delivery of postal mail to some countries in Central and South America, limited use of English as a first language) resulting in some delays in receipt of materials and understanding what is needed.

We identified submission of several LPU's (Least Publishable Units) in 2009 and tried to discourage this practice. We also strongly discouraged manuscripts for which the 'important' findings were published elsewhere. These issues are not easily discerned but reviewers can be helpful in identifying questionable manuscripts. We receive manuscripts (as do most journals) that were originally submitted elsewhere. We treat these manuscripts fairly but try to learn why they were discouraged by other journals. We also were threatened with legal action concerning author sequence on a paper after it was published. Signed copyright forms (showing author sequence) were available for all authors and the action was terminated. Thus, there are valid reasons why we insist on having signed copyright forms on file before any manuscript is published.

The editing and publication process has become more time consuming each year, as there are many details to consider. I understand why other journals have changed processes and procedures complete with large numbers of Associate or Assistant Editors and a variety of editorial staff. Everything is more complex and one must be alert to what is best for a particular situation.

Allen Press continues to be very helpful and to do outstanding work preparing and printing *The Wilson Journal of Ornithology*. Their work is deeply appreciated, as it makes us look competent. The support of WOS Council and the Publications Committee is also essential to making our life easier.

Clait E. Braun, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

Janet Hinshaw, WOS Librarian, has provided the following statistics regarding use of the Van Tyne Library and the status of the library.

Loans

Number of loans: three; number of members to whom loans were sent: three; number of photocopies or scans provided: six.

Acquisitions

Exchanges: A total of 120 publications was received by exchange from 198 organizations or individuals. We have lost several exchanges in the past few years and have had to subscribe to keep those journals current.

Gifts: We received 24 publications from 20 organizations.

Subscriptions: We also received 33 publications from 23 subscriptions. We spent a total of $660.84 on subscriptions in 2009.

Donations: A total of 13 items was received from members and friends. These included 12 journal issues and one translation. Donors included P. Ames and J. Hinshaw.

Purchases: one journal issue and three books, for $144.95 in credit from Buteo Books.

Dispersal

Back Issues. Due to lack of demand in recent years and having to clear out of the store room, we have disposed of the bulk of our stock of back issues of *The Wilson Bulletin.*

Gifts Sent Out: one book was donated to Dan Hanley of the University of Windsor.

Duplicates: 26 books were sold for $2,600.00 credit with Buteo Books.

We remind members that we can lend books or provide paper or electronic copies of articles from items in the library. The Google scanning project has not yet begun for the bird library, but is tentatively scheduled for fall/winter 2010. I thank our student worker, Theresa Gorman, for day-to-day operations, and our secretary, Bev Dole, for assistance with photocopying.

Jerome A. Jackson, *Chair*

REPORT OF THE PUBLICATIONS COMMITTEE

The Publications Committee of the Wilson Ornithological Society consists of Mary Bomberger Brown (chair), Richard Banks, Michael Hamas, Fred Lohrer, and Clait Braun (as editor of *The Wilson Journal of Ornithology*). During the past year, we focused our attention on three areas, all with the goal of continuing to improve the quality and stature of *The Wilson Journal of Ornithology.*

We acquired free access to *The Wilson Journal of Ornithology* on BioOne (www.bioone.org) for Wilson Ornithological Society members. We worked with Christina Berger at Allen Press and Christopher Schneider at the Schneider Group/ OSNA to transfer WOS member information to BioOne; there is now a link to BioOne on the Wilson Ornithological Society web page. This free society member access to BioOne offers us several benefits: (1) it offers a tangible benefit to membership; (2) it brings more attention to the society, potentially increasing membership; and (3) it increases journal usage. There is no cost to the Wilson Ornithological Society for this service.

The Table of Contents of *The Wilson Journal of Ornithology* is now distributed via e-mail to all OSNA members before the journal is published. Early release of the Table of Contents offers us several benefits: (1) it advertises *The Wilson Journal of Ornithology* and The Wilson Ornithological Society to OSNA members; (2) it helps members stay abreast of the journal contents; (3) it reminds members, including lapsed members, to renew their society membership; and (4) it encourages authors to consider submitting their manuscripts to the *Journal* for publication. There is no cost to The Wilson Ornithological Society for this service.

The guidelines for authors submitting manuscripts to *The Wilson Journal of Ornithology* and links to the guidelines on the web page were updated. The guidelines now clarify the use of the American Ornithologists' Union checklist for names of birds that occur in Mexico and the rest of North America, and the International Ornithological Congress checklist for names of birds that occur outside of North America. The preferred font for manuscript submissions has been clarified as have details of figure/illustration preparation.

We continue to work with the Schneider Group/ OSNA to address the issue of the size of the print run for *The Wilson Journal of Ornithology.* We have not pursued adding a Twitter feed to The Wilson Ornithological Society web page, although the service is available through OSNA at no cost to the society.

Mary Bomberger Brown, *Chair*

REPORT OF THE SCIENTIFIC PROGAM COMMITTEE

The Committee on the Scientific Program consisted of WOS Second Vice-President Robert L. Curry (Chair), Robert C. Beason, Susan B. Smith, and Scott H. Stoleson. Paper sessions were moderated by Greg Farley, Elise Ferree, Mary Garvin, Jerome A. Jackson, Rachel Muheim, Timothy J. O'Connell, Daniel Shustack, Charles Smith, Lindsay A. Walters, and Douglas W. White. The symposium on new perspectives in migratory physiology and energetics was moderated by Susan B. Smith and Mark E. Deutschlander, and the symposium on the effects of energy development on birds was moderated by Scott H. Stoleson.

PAPER SESSIONS

Symposium: New Perspectives in Migratory Physiology and Energetics

Ulf Bauchinger and Scott McWilliams, University of Rhode Island, "Tissue turnover rate

determines extent of phenotypic flexibility in organ size of migrating birds.''

Lauren S. MacDade and Paul G. Rodewald, The Ohio State University, and Kent A. Hatch, Long Island University, ''Contributions of emergent aquatic insects to refueling by spring migrant songbirds.''

Scott R. McWilliams, University of Rhode Island, and Barbara Pierce, Sacred Heart University, ''The fat of the matter: how dietary fatty acid composition affects energy expenditure of birds during migration.''

Jen Owen, Michigan State University, ''Links between energetic condition, immune function, and disease susceptibility in migrant birds.''

Edwin Price, University of Western Ontario, ''Towards a theoretical framework for avian fat storage.''

Robert J. Smith, University of Scranton, ''Arrival and transition into the breeding period: the fitness consequences of timing and condition for a landbird migrant.''

Symposium: The Effects of Energy Development on Birds

Gregory A. George, James Sheehan, and Petra Bohall Wood, West Virginia Cooperative Fish and Wildlife Research Unit, and Harry Edenborn, National Energy Technology Laboratory, ''Avian responses to gas well development in West Virginia.''

Nels Johnson, The Nature Conservancy, ''Can natural habitats survive the energy revolution?''

Todd Katzner, National Aviary, Trish Miller and Michael Lanzone, Powdermill Nature Reserve, David Brandes, Lafayette College, and Robert Brooks, Pennsylvania State University, ''Threats to migrating Golden Eagles from development of wind energy.''

Jeff Larkin, Joseph Grata, and Joe Duchamp, Indiana University of Pennsylvania, and Laura Patton, Kentucky Department of Fish and Wildlife Resources, ''Developing guidelines for the creation of Golden-winged Warbler breeding habitat on reclaimed surface mines in southeastern Kentucky.''

Emily H. Thomas, Pennsylvania State University, ''Effects of oil and gas development on songbirds.''

Kim Van Fleet, Audubon Pennsylvania, ''Energy development and fragmentation effects.''

General Sessions

William H. Barnard, Norwich University, ''Blood parasites in overwintering Rusty Blackbirds.''

Sean R. Beckett, Glenn A. Proudfoot, and Mary Ann Cunningham, Vassar College, ''Large-scale movement and migration of Northern Saw-whet Owls.''

J. Alan Clark, Fordham University, ''Tracking birds migrating at night through an urban-rural corridor and quantifying the effects of light and noise pollution.''

Katie Clower, University Minnesota, ''The effects of rotational grazing on relative abundance of grassland songbirds.''

Robert L. Curry, Villanova University, ''Variation in chickadee morphology through time in a moving hybrid zone.''

Christine Eldredge, Brian Monaco, and Mark E. Deutschlander, Hobart and William Smith Colleges, ''Seasonal energetic differences between migratory, non-migratory, and irruptive songbirds.''

Harold Eyster, Chelsea, Michigan, ''Tolmie's MacGillivray's Warbler: the story of a name.''

Jeanne M. Fair, Los Alamos National Laboratory, and Ellen Paul, The Ornithological Council, ''Guidelines to the use of wild birds in research.''

Greg H. Farley, Andrée Brisson, Alex Galt, and Stephanie Kane, Fort Hays State University, ''Patterns in migratory songbird capture between 1966–1980 and 1995–2009 at an autumn banding station in the High Plains.''

George L. Farnsworth, Dorothy B. Engle, Brett E. Schrand, and Christopher C. Stobart, Xavier University, and Rebecca B. Desjardins, North Carolina State Museum of Natural Sciences, ''Seasonal and geographic variation in nestling sex ratio in the Northern Mockingbird.''

Elise Ferree and Janis Dickinson, Cornell University, ''Lifetime survival and reproductive success of extra-pair and within-pair Western Bluebirds (*Sialia mexicana*).''

James E. Garabedian and Frank Ammer, Frostburg State University, and J. Edward Gates, University of Maryland, ''Habitat associations of over-wintering birds in restored hayfields in the Manassas National Battlefield Park, Virginia.''

Douglas A. Gross, Pennsylvania Game Commission, ''Pennsylvania boreal conifer forests and their bird communities: past, present, and future potential.''

Jessie Hogue-Morgenstern and James Marshall,

Denison University, "The relationship of migrant avian frugivory and honeysuckle (*Lonicera*) management in the fall."

Jerome A. Jackson and Bette J. S. Jackson, Florida Gulf Coast University, "Winter association of birds with the invasive exotic Brazilian pepper (*Schinus terebinthifolius*)."

Gustavo Adolfo Londoño, University of Florida, "Breeding biology of five species of high elevation Andean tanagers."

Lawrence C. Long and James Marshall, The Ohio State University, "Survey of Lake Erie island passerine nest predation."

Christina Masco and Thomas D. Seeley, Cornell University, "Individuality and recognition in the Great Black-backed Gull, *Larus marinus*."

Adrian P. Monroe and Timothy J. O'Connell, Oklahoma State University, "Winter bird response to heterogeneity-based management in a tallgrass prairie."

Erica G. Mueller and John A. Smallwood, Montclair State University, "A spectrographic analysis of American Kestrel (*Falco sparverius*) vocalizations. Do broodmates sound more like each other than non-related broods?"

Rachel Muheim, Lund University, John B. Phillips, Virginia Polytechnic Institute and State University, Derring Hall, Blacksburg, Virginia, and Mark E. Deutschlander, Hobart and William Smith Colleges, "Sunrise and sunset polarized light cues calibrate the magnetic compass in migratory songbirds."

Christopher Norment, SUNY College at Brockport, "Fifteen years of research on grassland birds in New York State: habitat relations and management implications."

Timothy J. O'Connell and Andrew D. George, Oklahoma State University, "Influence of seeded, exotic grasslands on wintering birds in mixed-grass prairie."

Sarah E. Pabian and Margaret C. Brittingham, Pennsylvania State University, "Complex relationships between forest songbirds and soil conditions."

Monika Parsons and Frederick A. Servello, University of Maine, and Cynthia S. Loftin, USGS Maine Cooperative Fish and Wildlife Research Unit, "Quantifying incubation behavior of Common Eiders nesting on Jordan's Delight Island, Maine."

Joel Ralston, University of Albany, "Integrating species distribution models and genetic data to forecast the effects of climate change on genetic diversity in boreal birds."

Sonya Richmond and J. Malcolm, University of Toronto, E. Nol, Trent University, and D. Burke, Ontario Ministry of Natural Resources, "Influence of adult age on Rose-breasted Grosbeak nestling provisioning rates in stands harvested by single-tree selection."

Sarah T. Saalfeld and Warren C. Conway, Stephen F. Austin State University, David A. Haukos, Texas Tech University, and William P. Johnson, Texas Parks and Wildlife Department, "Nest success of Snowy Plovers in the Southern High Plains of Texas."

Matthew S. Savoca, David N. Bonter, Benjamin Zuckerberg, and Janis L. Dickinson, Cornell University, and Julie C. Ellis, Tufts Cummings School of Veterinary Medicine, "Nesting density an important factor affecting chick growth and survival in the Herring Gull (*Larus argentatus*)."

Richard R. Schaefer and D. Craig Rudolph, USFS Southern Research Station, "Southeastern American Kestrel nesting habitat and nestling provisioning in the West Gulf Coastal Plain."

Chad L. Seewagen and Christopher G. Guglielmo, University of Western Ontario, "Ovenbird spatial behavior at an urban stopover site: movement patterns, stopover durations, and the influence of arrival condition."

Daniel P. Shustack, Massachusetts College of Liberal Arts, and Amanda D. Rodewald, The Ohio State University, "Nest predation reduces benefits to early clutch initiation in an urbanizing landscape."

Dennis G. Siegfried, Daniel S. Linville, and David Hille, Southern Nazarene University, "Analysis of nest sites of the Resplendent Quetzal (*Paromachrus mociuno*): a relationship between nest and snag heights."

Charles R. Smith, Cornell University, "The elements of science-based, adaptive bird conservation and the public trust doctrine."

Marla L. Steele and Timothy J. O'Connell, Oklahoma State University, "Effects of cold front passage on migrant raptors at Shirakaba Pass, Nagano Prefecture, Japan, autumn 2000–2009."

Scott H. Stoleson, USFS Northern Research Station, "Does habitat choice in the post-breeding season affect physiological condition of forest-interior songbirds?"

Judit Ungvari-Martin, Ari Martinez, and Scott K. Robinson, University of Florida, "Variation in

understory forest bird communities of Amazonian forests on different soils."

Gretchen F. Wagner and Mark E. Hauber, CUNY Hunter College, "Patterns of Brown-headed Cowbird parasitism on Eastern Phoebes: a ten-year comparison."

Lindsey A. Walters, Canisius College, and Natalie Dubois and Thomas Getty, Michigan State University, "Influences of mate quality and population growth on House Wren clutch size."

Rebecca J. Whelan and Tera C. Levin, Oberlin College, Jennifer C. Owen, Michigan State University, and Mary C. Garvin, Oberlin College, "Short-chain carboxylic acids from Gray Catbirds (*Dumetella carolinensis*) uropygial secretions vary with testosterone levels and photoperiod."

Douglas White and E. Dale Kennedy, Albion College, "Gaps in nocturnal incubation in House Wrens (*Troglodytes aedon*)."

Whitney A. Wiest and W. Gregory Shriver, University of Delaware, and Hal Laskowski, U.S. Fish and Wildlife Service, "Development of a bird community integrity index to monitor salt marsh condition at national wildlife refuges."

Marie E. Wilson, Jordan M. Casey, David G. Haskell, and Nicholas Hollingshead, University of the South, "The effects of exurbanization on the food and habitat of Pileated Woodpeckers (*Dryocopus pileatus*)."

Stephanie G. Wright and Robert L. Curry, Villanova University, "Hybrid chickadee vocalizations change as the hybrid zone moves northward in southeastern Pennsylvania."

POSTERS

Aubrey Alamshah and Edward H. Burtt Jr., Ohio Wesleyan University, "Seasonal changes in maintenance behavior of the House Sparrow (*Passer domesticus*)."

Andrew C. Alba and Gregory B. Cunningham, St. John Fisher College, "The fox in the henhouse: responses of chickens (*Gallus domesticus*) to the scent of a predator."

Catherine C. Alsford and Dorothy I. Fatunmbi, Canisius College, Brenda S. Keith and Richard S. Keith, Kalamazoo Nature Center, and Sara R. Morris, Canisius College, "Does age matter? A study of whether age affects stopover ecology of migrant warblers."

Robert C. Beason, Accipiter Radar Corporation, "Remote radar monitoring of bird activity via the network."

Martyna Boruta and Mark E. Deutschlander, Hobart and William Smith Colleges, "Ultraviolet reflectance and age/sex variation in Yellow Warblers (*Dendroica petechia*)."

W. P. Brown and M. E. Zuefle, Kutztown University, "Are bird images returned from search engine results accurately identified?"

Jameson F. Chace, Salve Regina University, and Steven D. Faccio, Vermont Center for Ecostudies, "Evaluation of breeding habitat quality for a population in decline: the Canada Warbler in northeastern Vermont."

Kailey Chidester, Bethany Bashaw, and Mark E. Deutschlander, Hobart and William Smith Colleges, "Determining land quality for migratory birds near the Lake Ontario shoreline: a study of daily mass gain during fall and spring migration."

Kelly Fox, Alyssa Caffarelli, and Lindsey Walters, Canisius College, and Brian S. Maitner, Rice University, "Nest defense and parental investment in the House Wren."

Casey Franklin, Jordan Youngman, Mianna Molinari, and Mark E. Deutschlander, Hobart and William Smith Colleges, "Energetic condition of spring migrating North American warblers at a northern stopover site: a study of Breeding and Insurance hypotheses."

Samuel Georgian, Paul Overdorf, and Mark E. Deutschlander, Hobart and William Smith Colleges, "Determining the role of the Insurance Hypothesis in the stopover ecology of two kinglets and two flycatchers."

Erin Greenlee and Ian Hamilton, The Ohio State University, "Distributional shifts of breeding birds in Ontario, Canada."

Nathan Grosse, Christopher Norment, and Mark Norris, SUNY Brockport, and Heidi Kennedy, NY Department of Environmental Conservation, "Area effects removed: vegetation characteristics and grassland bird abundance in a western New York field."

Margret I. Hatch, Penn State Worthington Scranton, and Robert J. Smith, University of Scranton, "Annual variation in arrival of long-distant migrants and a comparison of first capture dates and condition between verified breeders and presumed migrants."

Jordan S. Kalish and Edward H. Burtt Jr., Ohio Wesleyan University, "Bacteria and fungi in the plumage of birds of prey."

Rachel Kushner, Christy Conley, and James S. Marshall, Denison University, "Patterns of inter-

ference competition in overwintering central Ohio birds.''

Anne Lugg, W. Brown, D. Alexander, M. Zuefle, and T. Underwood, Kutztown University, ''Aging House Wren nestlings based on feather tract development, wing chord, and head length.''

Mianna Molinari and Mark E Deutschlander, Hobart and William Smith Colleges, ''The influence of temperature on energetic condition in spring migrating warblers.''

Brad Mudrzynski and Christopher Norment, SUNY College at Brockport, ''Early successional habitat characteristics and fruit abundance influence stopover use of fall migrating songbirds.''

Laura M. Niczyporowicz and Todd J. Underwood, Kutztown University, and Roland R. Roth, University of Delaware, ''The effectiveness of constant effort mist-netting in estimating abundance and reproductive success of a Wood Thrush population.''

Nathan Olszewski, Kevin Sobol, and Lindsey Walters, Canisius College, ''Male response to egg color in the House Wren.''

Paul Overdorf and Mark E. Deutschlander, Hobart and William Smith Colleges, ''Using wing morphology and mass to model the potential flight distances of passerines at a stopover site near Lake Ontario.''

Benjamin J. Padilla, Ashley Ballou, and Gregory S. Keller, Gordon College, ''The effects of natural and human induced edges on foraging flocks of wintering songbirds in southern New England.''

Ashley N. Rathman and William P. Brown, Kutztown University, and Roland R. Roth, University of Delaware, ''The effect of Wood Thrush hosts on the survival of Brown-headed Cowbird eggs and nestlings.''

Susan B. Smith, Villanova University, ''An assessment of refueling rates and diet of songbirds during migratory stopover at the Braddock Bay Bird Observatory.''

Kevin Sobol, Nathan Olszewski, and Lindsey Walters, Canisius College, ''Egg color and female quality in the House Wren.''

Brynne A. Stumpe and Sara R. Morris, Canisius College, ''The effects of a residential wind turbine on bird behavior.''

Jason M. Townsend, SUNY College of Environmental Science and Forestry, and Charles T. Driscoll, Syracuse University, ''Mercury bioaccumulation in *Catharus* thrushes along an elevational gradient.''

Mitch Walters, Cornell University, Marcela Liljesthrom, Centro Austral de Investigaciones Cientificas, CADICONICET, Argentina, and Caren Cooper, Cornell University, ''Comparing female characteristics to egg and yolk size in the Chilean Swallow (*Tachycineta meyeni*).''

ATTENDANCE

ALABAMA: *Tuscaloosa*, Marie E. Wilson.

ARIZONA: *Tucson*, Clait E. Braun, Nancy J. K. Braun.

CALIFORNIA: *Concord*, Naho Kermeen.

DISTRICT OF COLUMBIA: Carla Dove.

DELAWARE: *Newark*, Whitney Wiest.

FLORIDA: *Gainesville*, Gustavo Londoño, Judith Ungvari-Martin; *Jacksonville*, Bynne Stumpe; *Naples*, Bette Jackson, Jerome Jackson.

INDIANA: *Bristol*, Doris Watt.

KANSAS: *Hays*, Andree Brisson, Greg Farley, Cate Healy.

MAINE: *Orono*, Monika Parsons.

MARYLAND: *Bethesda*, Ellen Paul; *Brandywine*, Rachael Kushner; *Columbia*, James Smith; *Frostburg*, James Garabedian.

MASSACHUSETTS: *Chilmark*, Allan Keith; *East Falmouth*, Ted Davis; *Haverhill*, Benjamin Padilla; *North Adams*, Daniel Shustack; *Pocasset*, John C. Kricher.

MICHIGAN: *Albion*, Dale Kennedy, Doug White; *Ann Arbor*, Bob Payne, Laura Payne; *Chelsea*, Harold Eyster; *East Lansing*, Jen Owen.

MINNESOTA: *Minneapolis*, Katie Clower.

MISSOURI: *Columbia*, Andrew Cox; *St. Louis*, William Condit.

NEW HAMPSHIRE: *Bow*, Christie Eldredge; *Manchester*, Jay Pitocchelli.

NEW JERSEY: *Lincoln Park*, Erica Mueller; *Lyndhurst*, Michael Newhouse; *Pennington*, Stephanie Wright; *Randolph*, John Smallwood, Mary Anne Smallwood.

NEW MEXICO: *Albuquerque*, Erin Greenlee.

NEW YORK: *Albion*, Brad Mudrzynski; *Armonk*, J. Alan Clark; *Brockport*, Nathan Grosse, Christopher Norment; *Bronx*, Oriana Chan, Kyle Wright; *Brooklyn*, Jesse Ross; *Buffalo*, Catherine Alsford, Lindsey Walters; *Geneseo*, Kristina Hannam; *Geneva*, Bethany Bashaw, Mark Deutschlander, Casey Franklin, Samuel Georgian, Becky Jones, Mianna Molinari, Brian Monaco, Paul Overdorf, Bob Taylor, Jordan Youngmann; *Grand Island*, Sara Morris, Kevin Sobol; *Hamburg*, Kelly Fox; *Hurley*, Kailey Chidester;

Ithaca, Caren Cooper, Elise Ferree, Jane Graves, Heidi Lovette, Christina Masco, Colleen McLinn, Matthew Savoca, Charlie Smith, Scott Sutcliffe, Jason Townsend, Mitch Walters; *Menands*, Joel Ralston; *New York*, Chad Seewagen; *Newburgh*, Gretchen Wagner; *Niagara Falls*, Dorothy Fatunmbi; *Poughkeepsie*, Glenn Proudfoot; *Rochester*, Andrew Alba; *Rye*, Christy Conley; *Utica*, Judith McIntyre; *West Seneca*, Alyssa Caffarelli, Nathan Olszewski.

OHIO: *Cincinnati*, Dottie Engle, George Farnsworth; *Columbus*, Lawrence Long, Paul Rodewald; *Delaware*, Aubrey Alamshah, Edward Burtt Jr., Jordan Kalish; *Granville*, Jessie Hogue-Morgenstern; *Medina*, Amanda Fawcett; *Oberlin*, Mary Garvin; *Sandusky*, Robert Beason; *Westerville*, James Marshall.

OKLAHOMA: *Edmond*, Dennis G. Siegfried; *Norman*, Tamaki Yuri; *Stillwater*, Adrian Monroe, Tim O'Connell, Marla Steele; *Tahlequah*, Mia Revels.

PENNSYLVANIA: *Barto*, George Gregory; *Carisle*, Kim Vanfleet; *Dunmore*, Margaret Hatch; *Erie*, Margaret Voss; *Harrisburg*, Nels Johnson; *Indiana*, Jeff Larkin; *Kutztown*, Bill Brown, Todd Underwood; *Levine*, Scott Stoleson; *Markleysburg*, Frank Ammer; *Mertztown*, Ann Lugg; *Orangeville*, Douglas Gross; *Philadelphia*, Laura Niczyporoxicz; *Pittsburgh*, Todd Katzner, Fred McCullough, Michael Sobkowiak; *Reading*, Ashley Rathman; *Scranton*, Rob Smith; *Sugar Grove*, Pam Stoleson; *University Park*, Sarah Pabian; *Villanova*, Bob Curry, Susan Smith; *Warren*, Emily Thomas; *Williamsport*, Nathan Frank;

RHODE ISLAND: *Kingston*, Ulf Bauchinger, Scott McWilliams; *Newport*, Jameson Chace.

TEXAS: *Nacogdoches*, Sarah Saalfeld, Rick Schaefer.

VIRGINIA: *Alexandria*, Dick Banks; *Shipman*, Allen Hale

VERMONT: *Northfield*, William Barnard; *Williston*, Sean Beckett;

CANADA, ONTARIO: *Ajax*, Sonya Richmond; *London*, Eddy Price; *Mississauga*, Silu Wang; *Newmarket*, Mike Van den Tillaart; *Simcoe*, Erica Dunn, David Hussell; *Toronto*, James Rising, Trudy Rising.

SWEDEN: *Lund*, Rachel Muheim.

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REVIEWERS FOR VOLUME 122

Referees are the life blood of a journal as editors depend on them to help identify manuscripts with merit and offer suggestions to improve the data analysis, overall science, and writing. These individuals receive little recognition but are extremely important in the process of improving the science and quality of what is published. We thank all of those listed below who served as referees for manuscripts processed (accepted and published, withdrawn, rejected) after 1 July 2009 through completion of the December 2010 issue of Volume 122. (Those shown in boldface reviewed more than one manuscript in this period.) The Wilson Ornithological Society and the editorial staff are indebted to and thank each person who served as a reviewer.—Clait E. Braun, Editor

K. P. Able, N. J. Adams, J. Aguilar-Amat, J. A. Ahumada, A. D. Anders, R. G. Anthony, D. P. Armstrong, E. Arriero, L. Aubry, **S. K. Auer**, J. K. Augustine, D. Badzinski, V. Baglione, M. C. Baker, G. Ballard, W. H. Baltosser, G. Barrantes, J. Bart, J. Bates, R. C. Beason, **G. Beauchamp**, M. Bekoff, J. R. Belthof, M. Benowitz-Fredericks, K. S. Berg, T. M. Bergin, M. Bidwell, R. O. Bierregaard, K. Bildstein, T. R. Birkhead, C. A. Bishop, **J. G. Blake**, J. A. Blakesley, L. A. Blanc, C. R. Blem, P. H. Bloom, C. W. Boal, C. E. Bock, E. K. Bollinger, J. S. Bolsinger, D. N. Bonter, T. A. Bookhout, C. A. Botero, W. S. Boyd, J. E. Bradley, L. A. Brennan, D. Brightsmith, D. W. Buden, **D. E. Burhans**, D. B. Burt, E. H. Burtt Jr., P. H. Butchko, C. J. Butler, B. S. Cade, T. Cade, C. Caffrey, J. W. Cain, S. Calme, B. R. Chapman, **J. Chaves-Campos**, **N. Chernetsov**, R. T. Chesser, R. Cintra, R. B. Clapp, W. Clark, C. E. Clarkson, N. J. Collar, **C. T. Collins**, J. C. Connelly, L. M. Conner, R. N. Conner, C. J. Conway, M. I. Cook, D. W. Coulton, R. Covas, J. Cox, S. Craig, E. R. A. Cramer, H. Q. P. Crick, A. Cruz, J. F. Cully, **F. J. Cuthbert**, L. D'Alba, W. E. Davis, D. K. Dawson, D. C. Dearborn, K. L. Decker, C. A. Delgado, M. M. Delgado, R. DeLotelle, E. P. Derryberry, A. Desrochers, T. L. DeVault, A. A. Dhondt, J. Diamond, A. S. Dolby, L. Dos Angos, C. J. Dove, W. Duckworth, K. M. Dugger, P. O. Dunn, J. B. Dunning Jr., W. R. Eddleman, B. A. Eichhorst, **J. C. Eitniear**, K. S. Ellison, L. Ellison, C. S. Elphick, A. Engilis Jr., **R. M. Erwin**, R. H. M. Espie, D. L. Euler, J. Faaborg, A. Farnsworth, T. W. Fawcett, E. Fernandez-Juricic, K. Fierro-Calderon, **J. Fjeldså**, C. R. Foster, M. S. Foster, R. M. Fraga, C. Francis, M. R. Francisco, P. C. Frederick, M. Frederiksen, R. W. Furness, G. A. Gale, V. Garcia, S. A. Gauthreaux, J. L. Gehring, D. D. Gibson, A. Giese, J. D. Gilardi, F. B. Gill, M. D. Giovanni, **C. B. Goguen**, H. B. Gomes, O. Gordo, J. B. Grand, D. J. Green, M. C. Green, R. Greenberg, P. D. Greger, M. Gregg, R. J. Gutiérrez, M. J. Guzy, J. H. Haffer, B. A. Hahn, P. B. Hamel, B. T. Hansen, A. Harmata, R. E. Harness, **J. B. C. Harris**, B. J. Hatchwell, W. M. Healy, S. G. Herford, **S. K. Herzog**, **E. J. Heske**, B. Heinrich, K. Higgins, J. E. Hines, K. A. Hobson, P. A. R. Hockey, R. W. Hoffman, C. S. Holling, R. T. Holmes, S. B. Holmes, G. Holroyd, J. P. Hoover, S. N. G. Howell, R. L. Hutto, L. D. Igl, **D. Ingold**, N. Itonaga, F. C. James, J. M. Jawor, J. R. Jehl, B. Jobin, D. H. Johnson, L. S. Johnson, O. W. Johnson, C. D. Jones, S. L. Jones, R. Kannan, P. Kappes, A. C. Kasner, J. L. Kellermann, C. Kellner, R. S. Kennedy, D. T. King, C. K. Kirkpatrick, G. Kirwan, N. A. Klaus, D. Klem Jr., S. T. Knick, G. Kobriger, W. D. Koenig, E. M. Kofoed, R. R. Koford, **N. K. Krabbe**, D. E. Kroodsma, J. A. Kushlan, H. Kylin, Q. Latif, S. C. Latta, J. J. Lawler, A. T. Lee, J. D. Ligon, J. Liguori, C. K. Lim, B. C. Livezey, P. E. Llambias, H. Lloyd, J. P. Loegering, J. T. Lokemoen, G. A. Londono, S. C. Lougheed, I. J. Lovette, J. Lowen, **P. E. Lowther**, J. E. Loye, R. S. Lutz, B. E. Lyon, E. A. MacDougal-Shackleton, R. H. F. Macedo, J. N. Mager III, D. L. Maney, M. A. Marini, W. R. Marion, P. P. Marra, L. B. Martin, P. R. Martin, T. E. Martin, T. L. Master, P. Matyjasiak, **J. E. McCormack**, D. McCracken, S. McGehee, K. J. McGowan, A. Mee, D. J. Mennill, **J. M. Meyers**, B. Miła, K. E. Miller, B. A. Millsap, C. M. Miskelly, S. Mitra, **A. P. Møller**, C. E. Moorman, M. L. Morrison, R. I. G. Morrison, D. H. Morse, E. S. Morton, R. Moss, **R. L. Mumme**, T. G. Murphy, L. D. Murray, L. N. Naka, Z. Nemeth, S. A. Nesbitt, P. Newell, D. Newstead, N. Nielsen-Pincus, G. Niemi, **I. C. T. Nisbet**, R. Noske, K. P. Oh, G. H. Orians, L. W. Oring, S. J. Ormerod, J-M. Paillisson, J. D. Paruk, P. W. C. Paton, R. B. Payne, A. T. Pearse, N. G. Perlut, B. P. Peterjohn, L. J. Petit, **W. Post**, R. Poulin, B. Pranty, H. D. Pratt, T. Price, H. Prior, M. S. Pruett, B. Pugesek, C. M. Raley, C. J. Ralph, J. H. Rappole, J. T.

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Editor's Comments

The rate of submissions has increased in 2010 and it appears we will again receive >200 new manuscripts in the calendar year. This increases our need for reviewers. All manuscripts (very few are initially discouraged as inappropriate prior to the review process) are sent to a minimum of two subject area referees. We select potential reviewers from perusal of the Literature Cited, our file of subject area reviewers, and those offered by the authors of specific manuscripts. In a perfect world, we would expect to receive positive responses from about two of every three referees contacted to review a specific manuscript. This only rarely happens and we may have to contact up to 12 (or more) potential referees before we find someone to review a particular manuscript. This problem is not unique to our Journal as other editors have similar problems. The most recent Issue of *Science* (2010, 329: 1466) has a commentary (*Battling the Paper Glut*) on publishing and the responsibility of authors of published papers to be willing to review manuscripts. Their proposed solution would be to have authors of submitted manuscripts provide three reviews of other manuscripts.

Our goal is to provide reviews and editorial recommendations on suitability of manuscripts in a timely manner. Searching for someone to agree to review manuscripts slows the process. We ask those contacted about reviewing a manuscript to consider the need for competent and timely reviews. At the least, reviewers contacted are asked to respond either yes or no instead of not responding at all. The areas of delay in the process of publishing for *The Wilson Journal of Ornithology* are: reviewer availability, timeliness of reviews, and timeliness in author revision. Some manuscripts that are encouraged fail to be returned in a timely manner. Some never are returned and become *de facto* rejections or withdrawals.

We presently do not have a backlog of accepted manuscripts waiting for publication. Those being accepted in September and October into early November this year will be published in the March Issue of the next year with few exceptions.

Clait E. Braun
Editor, 2010

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Index to Volume 122, 2010

Compiled by Leslie A. Robb

This index includes references to genera, species, authors, and key words or terms. References are made to scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text, in addition to avian species. Nomenclature follows the *AOU Check-list of North American Birds* (Seventh Edition) and F. Gill and M. Wright and supplements through 2010 (*Birds of the World, Recommended English Names, Princeton University Press, Princeton, New Jersey, USA and Oxford, United Kingdom*). Reference is made to books reviewed and announcements as they appear in the volume.

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